For Reference

NOT TO BE TAKEN FROM THIS ROOM

Ex Libris
Universitatis
Albertaensis

THE UNIVERSITY OF ALBERTA

THE INSECT COMMUNITY ASSOCIATED WITH ROSE GALLS OF *DIPLOLEPIS POLITA* (CYNIPIDAE, HYMENOPTERA)

by

JOSEPH DAVID SHORTHOUSE

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ENTOMOLOGY

EDMONTON, ALBERTA

FALL 1970

Thesis
1970
S47

UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "The Insect Community Associated With Rose Galls of *Diplolepis polita* (Cynipidae, Hymenoptera)" submitted by Joseph David Shorthouse in partial fulfilment of the requirements for the degree of Master of Science.

Date Fall 1970

Autobiography

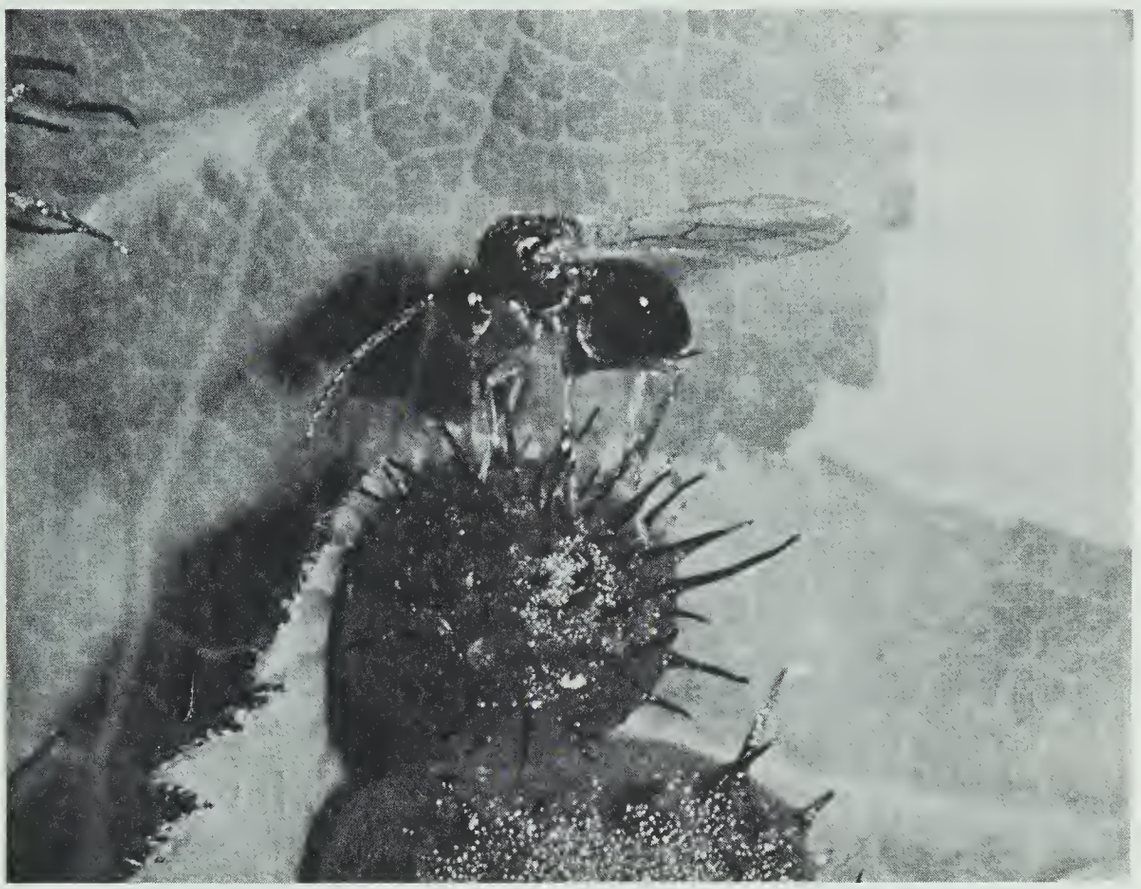
I was born in Lethbridge, Alberta, November 20, 1946. My formal schooling, grades 1-12, were spent in the Lethbridge School System. My early interest in entomology was stimulated by Dr. R. I. Larson while I was a member of her Junior Science Club of Lethbridge for 5 years. Under her encouragement and guidance I entered and won 6 awards in various categories of the insect collection competition sponsored by the Entomological Society of Alberta. During high school my interest in insect galls was stimulated through summer employment under Dr. A. M. Harper at the Canada Agriculture Research Station, Lethbridge. In 1963 I was adjudicated the Grand Award at the Lethbridge and District Science Fair, with a project entitled, 'Insect Galls of Southern Alberta'. I entered the University of Alberta in 1965 and obtained my B.Sc. in general biological sciences in 1968. The summer of 1967 was spent at Lake Hazen on Ellesmere Island studying insect-plant relationships and thermoregulation of high Arctic butterflies. In the spring of 1968 I was admitted to the Faculty of Graduate Studies and began a study on the biology of rose galls under the direction of Dr. W. G. Evans. In the summer of 1970 I was awarded a National Research Council of Canada Bursary to continue my studies of insect galls at the University of Saskatchewan.

Digitized by the Internet Archive
in 2020 with funding from
University of Alberta Libraries

https://archive.org/details/Shorthouse1970

Abstract

The single chambered gall of *Diplolepis polita* (Ashmead) is initiated in early spring on immature leaves of *Rosa acicularis* Lindl. (Rosaceae). The succulent gall tissue, consisting of four distinct layers, attracts five additional species. Gall initiation and developmental morphology are discussed. Most gall formers are replaced by the inquiline *Periclistus pirata* (Osten Sacken) (Cynipidae) which is the main food source of later entomophagous inhabitants. The interrelationships and seasonal changes in abundance of each species in the community are discussed. A comparison is made between the growth of *D. polita* inhabited galls and *P. pirata* inhabited galls. Galls containing *P. pirata* are enlarged and structurally modified. Entomophagous species of the community are *Eurytoma longavena* Bugbee (Eurytomidae), *Glyphomerus stigma* (Fabricius) (Torymidae), *Torymus bedeguaris* (Linnaeus) (Torymidae), and *Habrocytus sp.* (Pteromalidae).



Periclistus pirata (O.S.) ovipositing in an immature gall of Diplolepis polita (Ashmead). George Lake, Alberta. July 31, 1969.

Acknowledgements

I would like to thank the following people who have contributed much of their time to the completion of this thesis. W. G. Evans, chairman of my committee, provided continued encouragement, aid, and guidance throughout the study. G. E. Ball offered his advice on many occasions. B. Hocking, A. M. Harper, and D. D. Cass read and criticized the manuscript and offered many helpful suggestions. J. S. Scott helped with the illustrations and photography.

I thank fellow students T. L. Erwin, D. M. Rosenberg, H. Goulet, R. E. Leech, and V. K. Sehgal for their helpful suggestions. I also wish to thank my companions at the George Lake Field Station, A. W. Thomas, A. C. Carter, H. Goulet, and especially summer assistant N. R. Chymko. I am indebted to Mr. E. Donald and family, neighbours of the field station, for the numerous courtesies and services they provided. Successful operation of the field station was in many ways due to their unfailing co-operation.

I am also grateful to the following for identifying specimens: O. Peck, J. R. Barron, and M. Ivanochko (Cynipidae, Torymidae, and Pteromalidae), R. E. Bugbee (Eurytomidae), R. J. Lyon (Cynipidae), and W. H. Lewis (Rosaceae).

Finally I wish to thank the Boreal Institute of the University of Alberta for providing a grant-in-aid for the summer of 1969.

Table of Contents

List of Tables ix

List of Figures x

I. Introduction 1

A) Cecidology 1

B) Study Area 5

C) The Genus *Diplolepis* 5

D) *Diplolepis polita* (Ashmead) and Its Gall 7

II. The *Diplolepis polita* Gall Community 12

A) Biology of Gall Inhabitants 12

a) Introduction 12

b) Methods 15

c) Life Cycles of Gall Inhabitants 18

i) *Diplolepis polita* (Ashmead)
ii) *Periclistus pirata* (Osten Sacken)
iii) *Eurytoma longavena* Bugbee
iv) *Glyphomerus stigma* (Fabricius)
v) *Torymus bedeguaris* (Linnaeus)
vi) *Habrocytus sp.*

B) Community Studies 45

a) Introduction 45

b) Methods 46

c) Results and Discussion 46

III. Gall Growth and Developmental Morphology 56

A) Gall Growth Studies 56

a) Introduction 56

b) Methods 56

c) Growth of *D. polita* Inhabited Galls 57

d) Growth of *D. polita* Galls inhabited by *P. pirata* 61

B) Gall Developmental Morphology 68

a) Introduction 68

b) Materials and Methods 69

c) Gall Induction 70

d) Development of the *D. polita* Gall 71

e) Development of *P. pirata* Modified Galls 79

C) Gall Senescence and Abscission 81

IV. General Discussion and Conclusions 85

V. References Cited 90

List of Tables

Table 1. Incidence of *Periclistus pirata* eggs and larvae in the galls of *Diplolepis polita* 24

Table 2. Incidence of *Eurytoma longavena* eggs, larvae, and pupae in galls of *Diplolepis polita* 30

Table 3. Incidence of *Glyphomerus stigma* eggs and larvae in galls of *Diplolepis polita* 34

Table 4. Incidence of *Habrocytus sp.* larvae in the galls of *Diplolepis polita* 40

Table 5. Mean diameters of galls containing one larva of *Diplolepis polita* 60

Table 6. Mean diameters of *Diplolepis polita* galls containing eggs or larvae of *Periclistus pirata* 64

List of Figures

Fig. 1. Cluster of immature *Diplolepis polita* galls 9

Fig. 2. Mature galls of *Diplolepis polita* 9

Fig. 3. Gall inhabited only by *Diplolepis polita* 17

Fig. 4. Gall modified by *Periclistus pirata* 17

Fig. 5. Gall modified by *Eurytoma longavena* 17

Fig. 6. Gall modified by *Glyphomerus stigma* 17

Fig. 7. Mature larva of *Diplolepis polita* 41

Fig. 8. Mature larva of *Periclistus pirata* 41

Fig. 9. Mature larva of *Eurytoma longavena* 41

Fig. 10. Mature larva of *Glyphomerus stigma* 41

Fig. 11. Mature larva of *Habrocytus sp.* 41

Fig. 12. Mandible of *Diplolepis polita* 42

Fig. 13. Mandible of *Periclistus pirata* 42

Fig. 14. Mandible of *Eurytoma longavena* 42

Fig. 15. Mandible of *Glyphomerus stigma* 42

Fig. 16. Mandible of *Torymus bedeguaris* 42

Fig. 17. Mandible of *Habrocytus sp.* 42

Fig. 18. Oviposition periods recorded for species associated with *Diplolepis polita* galls 43

Fig. 19. Spring emergence from 300 *Diplolepis polita* galls stored under laboratory conditions 44

Fig. 20. Percentages of galls containing members of the *Diplolepis polita* gall community 52

Fig. 21. Incidence of empty *Diplolepis polita* galls 53

Fig. 22. Incidence of species in the *Diplolepis polita* gall community expressed as percentage of the total populations of gall inhabitants 54

Fig. 23. Food web of species associated with the *Diplolepis polita* gall community 55

Fig. 24. Seasonal change in the numbers of immature *Diplolepis polita* galls less than 4.0 mm. in diameter 65

Fig. 25. Seasonal change in the mean size of galls containing a single *Diplolepis polita* larva compared to galls containing *Periclistus pirata* eggs or larvae only 66

Fig. 26. Growth curves of *Diplolepis polita* galls inhabited by various members of the gall community . . . 67

Fig. 27. Cross section of *Rosa acicularis* bud 72

Fig. 28. Longitudinal section of *Rosa acicularis* leaf primordium 72

Fig. 29. Longitudinal section of *Rosa acicularis* leaf 72

Fig. 30. Process of encasing *Diplolepis polita* larva in gall cavity 75

Fig. 31. Section of immature gall showing cell arrangement and cells damaged by *Diplolepis polita* larva 75

Fig. 32. *Diplolepis polita* larva encased in gall cavity 75

Fig. 33. Section of gall wall showing differentiation into 4 zones 78

Fig. 34. Feeding damage of *Glyphomerus stigma* larva 78

Fig. 35. Mature gall showing completion of differentiation 78

Fig. 36. Immature gall damaged by ovipositor of *Periclistus pirata* 80

Fig. 37. Gall tissue influenced by feeding of *Periclistus pirata* larva 80

Fig. 38. *Periclistus pirata* larva surrounded by nutritive zone cells 80

Fig. 39. Percentage of galled leaves with necrotic tissue in collections of spring initiated *Diplolepis polita* galls 84

Fig. 40. Rate of gall maturation of spring initiated *Diplolepis polita* galls 84

Fig. 41. Rate of gall abscission of spring initiated *Diplolepis polita* galls 84

I. Introduction

A) Cecidology

Cecidology, the study of plant galls, has long been a subject of great interest to biologists. Although galls have been mentioned in the literature since ancient times (Hippocrates, 406-377 B.C., wrote on the medical properties of galls) it was not until the late eighteenth century that any attempt was made to explain the connection between galls and the insects found in them. Malpighi (1687) was probably the first to explain that the stimulus for gall formation was of animal origin. Cosens (1915) reviewed the older gall literature in a paper in which he discussed the founding of cecidology. Plumb (1953) also presented an excellent review of early cecidological literature and explained the development of controversial theories concerned with the source of gall forming stimulus, site of action, and gall developmental morphology.

Although a great deal of literature on insect galls has been amassed, much of it has been of a systematic nature only. Most cecidological workers in North America have occupied themselves with the classification of galls and gall insects and have disregarded fundamental problems such as gall initiation, developmental morphology, and inter-relationships of the inhabitants composing the gall communities. Checklists are prominent in North American cecidological literature and the most popular is by Felt (1940). The first major contributions to aspects such as gall anatomy have appeared within the past 80 years. Important contributors to this field have been Cook (1904, 1909, 1923), Cosens (1912), Kostoff and Kendall (1929), Küster (1911), and Wells (1916). For reviews of such

subject matter, see Plumb (1953), Mani (1964), and Buhr (1965).

Insect galls can be defined as atypical growths produced by plants in response to a foreign stimulus. This stimulus, of either chemical or physical nature, or both, can be provided by the larva or the adult gall former. Gall formers are found in at least 8 insect orders, but the majority are restricted to the families Cecidomyiidae and Cynipidae. Of the 1,280 gall formers in North America, about 38% belong to the Order Hymenoptera. 91% of the Hymenoptera gall formers belong to the family Cynipidae, the galls of which are recognized by all students of cecidology as the most remarkable in variety and complexity.

For gall development to occur, the life cycle of the gall former must be synchronized with the optimum galling conditions of the plant. One prime requisite for gall formation is the presence of meristematic tissue. The plant tissue must be in such a condition that the foreign stimulus can alter normal growth patterns. Stimulus for gall initiation can be supplied by either feeding activities of the adults (i.e. aphid galls), oviposition activities of the adult (i.e. sawfly galls, *Pontania* species) or by larval feeding activities (i.e. Cecidomyiidae and Cynipidae). Malyshev (1968) suggested that gall wasps can convert relatively differentiated tissue back into the meristematic state. Wells (1920) suggested that the gall former actually causes the dedifferentiation of host tissue, preventing the normal expression of host characters. Once dedifferentiation has occurred, stimuli from the insects cause the gall to grow into its specific shape. All galls, especially the more complex, have characteristic shapes and structures. The morphological character of a gall depends upon the genus of insect producing it rather than upon the

plant on which it is produced. Kinsey (1920b) suggested that many gall-causing Hymenoptera may be more readily identifiable by their galls than by their own morphological characters.

Although a few gall insects are found on more than one host species, most are specific to a single host genus. Cynipids have found optimal conditions on the oaks since 86% of the known species are associated with this genus. Malyshev (1968) suggested that this can be attributed to the fact that oaks are slow growing and have shoots that stay fresh and susceptible to galling for a long time. Most of the remaining cynipid species are associated with members of Rosaceae and 7% of these are restricted to the genus *Rosa*. A possible explanation for this might be Malyshev's suggestion that primitive Cynipidae caused galls on common ancestors of Rosales and Fagales and the two orders subsequently separated.

Galls are not evenly distributed on various parts of host plants. Besides being host specific, gall formers restrict themselves to specific plant organs. Mani (1964) reported that 5% of the known cynipid galls on *Quercus* form on the roots, 22% on branches, 2% on flowers, 4% on acorns, and about 63% on leaves. He also reported that over 80% of the galls on Rosaceae are formed on leaves.

Kuster (1911) distinguished two kinds of galls based on structural morphology. He termed the more primitive galls the kataplasmas and those more structurally complex, the prosoplasmas. Both terms have received wide usage in the literature. The kataplasmic galls (i.e. those caused by aphids) are characterized by a lack of both definitive tissues and a constant external shape. Kataplasmic galls are composed of homogeneous parenchyma cells, show little differentiation, and are structurally similar

to the meristematic tissues from which they develop. Prosoplasmic galls are characterized by a definitive size and form and their tissues, differentiated into well defined zones, are fundamentally different from the normal host tissue. The majority of cynipid galls are prosoplasmic. Wells (1921) presented evidence that prosoplasmic galls were phylogenetically derived from kataplasmic galls.

Gall structure depends on many factors, including time of oviposition and number of eggs laid in one area. Galls developing with one larva present are termed monothalamous and those containing several larvae are termed polythalamous. In polythalamous galls, each larva is individually surrounded by plant tissue. The presence of inquiline larvae in self-produced inner chambers may give a monothalamous gall the appearance of being polythalamous. Inquilines are defined as organisms that inhabit galls but do not directly interfere with the welfare of the gall former.

To my knowledge, little work has been done on the biology of insect galls in Alberta. There has yet to be a checklist compiled for the galls of Alberta and Western Canada. Only the aphid galls have received attention (Harper, 1959a, 1959b, and 1966; Cumming, 1968). A. C. Kinsey, in several of his works, mentioned receiving galls from Calgary, Alberta. Weld (1926) recorded that a worker in Toronto received galls of *D. bicolor* (Harris) and *D. multispinosus* (Gillette) from Calgary. All species studied in this present work are new locality records for Alberta and greatly extend known distributions.

It is my objective in this thesis to investigate the inter-relationships of the insects associated with the gall of *D. polita* (Ashm.) and attempt to determine how they modify structures of the host leaf.

B) Study Area

All field work was conducted at the Department of Entomology George Lake Field Station, 40 miles N.W. of Edmonton, Alberta (53° 57' N, 114° 06' W). All galls studied were found within the one square mile field station situated on the southern margin of the boreal mixed forest subzone (LaRoi, 1968). Fire is an important feature of the boreal mixed forest subzone and has influenced the ecology of George Lake. The forest is essentially untouched, with only some isolated logging prior to 1930. *Ledum groenlandicum* Oeder bogs and *Carex* species meadows are found in several places. There are a few open areas which allow bush stratum species to grow densely. Principal trees of the upper stratum are *Populus balsamifera* L. and *P. tremuloides* Michx. Other trees present, but less common, are *Betula papyrifera* Marsh., *Picea glauca* Moench., *Alnus tenuifolia* Nutt., and several species of *Salix*. The bush stratum is more diverse and the dominant species are *Rosa acicularis* Lindl., *Rosa woodsii* Lindl., *Amelanchier alnifolia* Nutt., *Cornus stolonifera* Michx., *Ribes lacustre* Pers., and *Viburnum edule* Michx. Common herbs are *Epilobium angustifolium* L., *Heracleum lanatum* Michx., and several species of *Solidago*.

C) The Genus *Diplolepis*

Weld (1957 and 1959) gave an excellent description of the family Cynipidae with keys to the subfamilies and genera. The main character used to separate the genus *Diplolepis* is the plowshare-shaped hypopygium. Kinsey (1920b) gave data on the phylogeny of the cynipid genera and

presented biological characters of each. All *Diplolepis* species are restricted to forming galls on *Rosa*.

Felt (1940) recorded 25 species of *Diplolepis*, as well as many varieties, as occurring in North America. There are now about 30 known species and two of these have been introduced (*D. mayri* Schl. and *D. rosae* L.). Undoubtedly many species remain to be described and a complete revision of the genus may show many of the existing names to be synonyms.

There is considerable confusion in the literature as to which generic name should be applied to cynipids forming galls on *Rosa*. The generic name *Rhodites* Hartig has been used extensively in cynipid literature, but Rohwer and Fagan (1917) established that *Diplolepis* Geoffroy had priority. Because *Rhodites* and *Diplolepis* are isogenotypic, *Rhodites* disappears in synonymy. Some Europeans still use *Rhodites* as there is sentiment for having it placed on the conservanda list. Kinsey and Ayres (1922) were the first North Americans to use *Diplolepis*. When Felt (1940) republished his North American checklist of galls, he also changed to *Diplolepis*. Weld (1952) reviewed the nomenclature problem and recognized Geoffroy (1762) as the author. Krombein (1958) listed Fourcroy (1785) as the author of *Diplolepis* and probably obtained this from Weld (1957), but both authors must be mistaken. Eady and Quinlan (1963) again listed Geoffroy as the author.

I have collected 8 different *Diplolepis* galls at George Lake, but at present have only three determined (*D. polita*, *D. bicolor*, and *D. multispinosus*).

D) *Diplolepis polita* (Ashmead) and Its Gall

Diplolepis polita was described by Ashmead (1890) as forming galls on the leaves of *Rosa californica* Cham. and Schlecht. He examined specimens from California, Dakota, and Colorado, but gave no specific type locality. *D. polita* has been found only in North America, although two European species form similar galls (*D. mayri* Schl. and *D. eglanteriae* Hartig). Ashmead stated that both males and females of *D. polita* are entirely black, but the specimens I reared and the two I examined from California have light brown abdomens. In his brief description, Ashmead mentioned receiving galls from Cockerell who used the manuscript name *spinosellus*. Cockerell (1890) stated that *D. spinosellus* was a new species, but gave no description of the gall former or the gall. Muesebeck et al. (1951) declared *spinosellus* Cockerell invalid. Krombein and Burks (1967) reinstated the name, but gave no reference to descriptions of the gall former or the gall. Fullaway (1911) also described the galls of *D. bicolor* and *D. polita* and their gall formers. According to Weld (1952) Fullaway misidentified the *D. polita* adults and instead considered them *D. bicolor*. Weld examined Fullaway's specimens and found that those labelled *D. bicolor* were actually *D. polita*. Beutenmuller (1922) also obtained some of Fullaway's specimens described as *D. bicolor* and, realizing they were not *D. bicolor*, proposed the name *D. occidentalis*. Weld (1952) examined Beutenmuller's *occidentalis* and confirmed the synonymy.

In 1968 and 1969, the gall of *D. polita* was the most common rose gall at George Lake. On a 1968 collecting trip to the Peace River Block in Northern Alberta and British Columbia, this gall was again the most

common of all rose galls collected. Previously the most northern locality known was Ashland, Oregon (Bugbee, 1951). I have yet to find this gall near Lethbridge, Alberta, although I have collected extensively in the area. *D. polita* appears restricted to Western North America. Weld (1957) recorded it from the Pacific coast but does not mention it (1959) as occurring in Eastern United States. *D. polita* is not mentioned in any of the Eastern North America checklists.

The gall of *D. polita* is small, spherical, monothalamous, and is minutely spinulose and sometimes tuberculose. All *D. polita* galls I collected were found on the upper surface of the leaflets (Figs. 1 and 2), although McCracken and Egbert (1922) stated that the gall can also be found on the stems. Nothing has previously been recorded on the anatomy of the gall, other than brief comments such as by Beutenmuller (1907), who mentioned that the gall is thin walled and hollow. McCracken and Egbert (1922) were the first to establish that the gall was monothalamous. My histological studies showed the gall to be prosoplasmic for the wall tissue is composed of four well defined zones (Fig. 35). The largest number of galls I found on one leaf was 39. Of all the galled leaves collected in the spring, 61% were host to 5 galls or less. Galls growing close to one another often coalesce.

Two groups of *D. polita* galls appear at George Lake in one season. Most galls appear in the early spring on rose bushes from previous years and in this study are referred to as spring initiated galls. Another group of galls appears later in the season on new sucker shoots (Section III Ac). Although the eggs of spring initiated and sucker shoot galls are probably laid at the same time, it appears that some factor suppresses development of sucker shoot galls.

1

2

Figs. 1 and 2. 1. Cluster of immature Diplolepis polita galls on leaflets of Rosa acicularis Lindl. George Lake, Alberta. June 23, 1969. 2. Mature galls of Diplolepis polita on Rosa acicularis leaflet. Note necrosis near galls. George Lake, Alberta. August 10, 1969. Accompanying scale lines equal 1.0 cm.

Galls growing under various physiological conditions are different in colour. The amount of sunlight received by the plant seems to be the factor which determines gall colour. Cosens (1912) stated that galls of *Pontania pomum* Walsh (Family Tenthredinoidea) are poorly coloured if they grow in deeply shaded areas. *D. polita* galls growing under normal conditions, in the shade of *Populus* species, are generally of a light greenish-yellow colour. Galls on plants growing in open spaces such as meadows, roadsides, and burned over areas, are often a bright red colour, especially when they are immature. Galls initiated later in the season and those growing in darkly shaded areas may be creamy coloured or even white. Niblett (1943) noted this for the galls of *D. eglanteriae* Htg. and *D. rosarum* Gir. As the *D. polita* galls mature, they become brown in colour (Section IIIC).

The gall of *D. polita* is similar to that of *D. bicolor* and *D. nebulosus* (Bassett). Ashmead (1890) was the first to mention the similarities of these three and also pointed out that *D. bicolor* was different mainly in spine length. Beutenmuller (1907) stated that *D. polita* and *D. nebulosus* may prove to be identical. Bassett (1890) described the gall of *D. nebulosus* as forming on the underside of rose leaves but otherwise similar to the *D. polita* gall. A more detailed examination of the two species and their galls may prove Beutenmuller's assumption correct.

In any study concerned with insect galls, it is vital that careful attention be paid to the accurate identification of host plants. *Diplolepis* species are restricted to *Rosa*, although several species can form galls on more than one host species. Niblett (1943) recorded *D. eglanteria* on 7 *Rosa* species. Harrison (1922) exposed *D. rosae* L. to 16 species of *Rosa* and found that oviposition took place only on the members of one section.

The three species of rose found in Alberta are *R. acicularis* Lindl., *R. woodsii* Lindl., and *R. arkansana* Porter, all belonging to section Cinnamomeae. Lewis (1957) stated that rose species are one of the most difficult groups to separate into distinct species. Species hybridize with ease giving fertile offspring, and the wide range of morphological variation contributes to identification problems. Two species, *R. acicularis* and *R. woodsii*, are found at George Lake and are difficult to distinguish. *D. polita* were found only on *R. acicularis* at George Lake, although in Western United States it causes galls on *R. californica*. *R. acicularis* is more common than *R. woodsii* at George Lake and is generally taller, less bushy, and has larger leaflets. *R. woodsii* flowers later in the season than does *R. acicularis* and usually has more densely spined stems. Lewis (1959) illustrated the Holarctic and North American distribution of *R. acicularis* and stated that it has the most extended native range of any species in the genus. *R. acicularis* is native to Northern Europe, Asia, and North America.

II. The *Diplolepis polita* Gall Community

A) Biology of Gall Inhabitants

a) Introduction

The inter-relationships of insect gall inhabitants constitute one of the most important ecological aspects of cecidology. Because of their localized concentrations of nutritive plant tissues, insect galls are often inhabited by numerous species besides the gall former. One European gall (Mani, 1964) is reported to have over 75 species associated with it. The present study investigates 5 species found associated with the gall of *D. polita*. These 5 species are *Periclistus pirata* (O.S.), *Eurytoma longavena* Bugbee, *Glyphomerus stigma* (Fabricius), *Torymus bedeguaris* (Linnaeus), and *Habrocytus sp.*

One of the first tasks in studying the relationships of gall insects is to classify each species as to its feeding habit. Cynipid gall formers are phytophagous for their entire larval stage. Both phytophagous and entomophagous species are found in the *D. polita* gall. Some gall inhabitants feed on gall tissues but do not harm the gall former and have been termed inquilines. Mani (1964) suggested that inquilines were originally gall forming species and have become secondarily specialized to life in galls of other species. Muesebeck et al. (1951) listed the species of *Periclistus, Ceroptres, Synergus,* and *Euceroptres* as being guests in insect galls. The term inquiline is derived from the Latin 'inquilinus' meaning tenant or guest. Few workers have used the term inquiline in a similar manner and as a result there is confusion as to the correct usage. Malyshev (1968) and Smith (pers. comm.) considers all species other than the gall former as inquilines. Triggerson (1914)

called a *Synergus* species an inquiline even though it mines from chamber to chamber devouring the gall forming larvae. Species that inhabit galls and feed on the gall former can hardly be considered guests. I use the term inquiline in referring to gall inhabitants that feed on gall tissues but do not harm the gall formers. Some inquilines form irregular cavities inside the thick walls of their host gall (Sternlicht, 1968) and do not come in contact with the gall forming larvae. Malyshev (1968) gave other examples of inquilinism. *Periclistus pirata*, associated with the gall of *D. polita*, does not suitably fit the above definition of an inquiline. Although the larvae feed only on gall tissues, their presence replaces the larva of *D. polita* (Section IIAcii). *P. pirata* might be considered a true inquiline if it inhabited polythalamous galls where it would be unlikely that all cecidozoans would be destroyed. Osten Sacken (1865) was one of the first workers to question the inquilinous behavior of *Periclistus* species. Lyon (1969) stated that the inquiline *Euceroptres maritimus* Weld develops inside the gall of *Callirytis quercussuttonii* Bassett (Family Cynipidae) and suggested that it may be a predator rather than a 'guest'.

There is little uniformity in the literature as to the usage of terms associated with entomophagous species inhabiting galls. Such common terms as parasite and predator are often misused. Smith (1916) distinguished parasites and predators based on the number of hosts required to complete development. He defined parasitic insects as those which pass their entire larval stage within or upon a single host and predacious insects as those which require more than one host to complete development. He also noted that a distinction between parasitism and predatism is of limited importance and it is wise to keep in mind that many species are

called parasites only because they belong to parasitic groups and not by reason of their feeding behaviour. Many cecidologists use the term predator only when referring to birds and mammals which break into galls. Doutt (1959) discussed usage of the term 'parasitoid' in distinguishing a specialized group of parasites, but this term has not been widely accepted. Doutt also defined parasites that feed externally as ectoparasites. *Habrocytus sp.* is an ectoparasite by Doutt's definition and I accept this use of the term. I found no internal parasites associated with the inhabitants of the *D. polita* gall. *E. longavena*, *G. stigma*, and *T. bedeguaris* require more than one host to complete their development. I accept Smith's definition of the term and prefer to call these species predators rather than parasites. Blair (1944 and 1945a) described the larvae of *E. rosae* L. as being predacious rather than parasitic, but described *G. stigma* and *Torymus sp.* as being ectoparasites. Askew (1961) stated that the situation where chalcidoid species consume more than one host is unusual. He suggested that it is best not to use the term predator for such relationships and thus avoid unnecessary complications. I have often observed such relationships in various *Diplolepis* galls and disagree with Askew's suggestion.

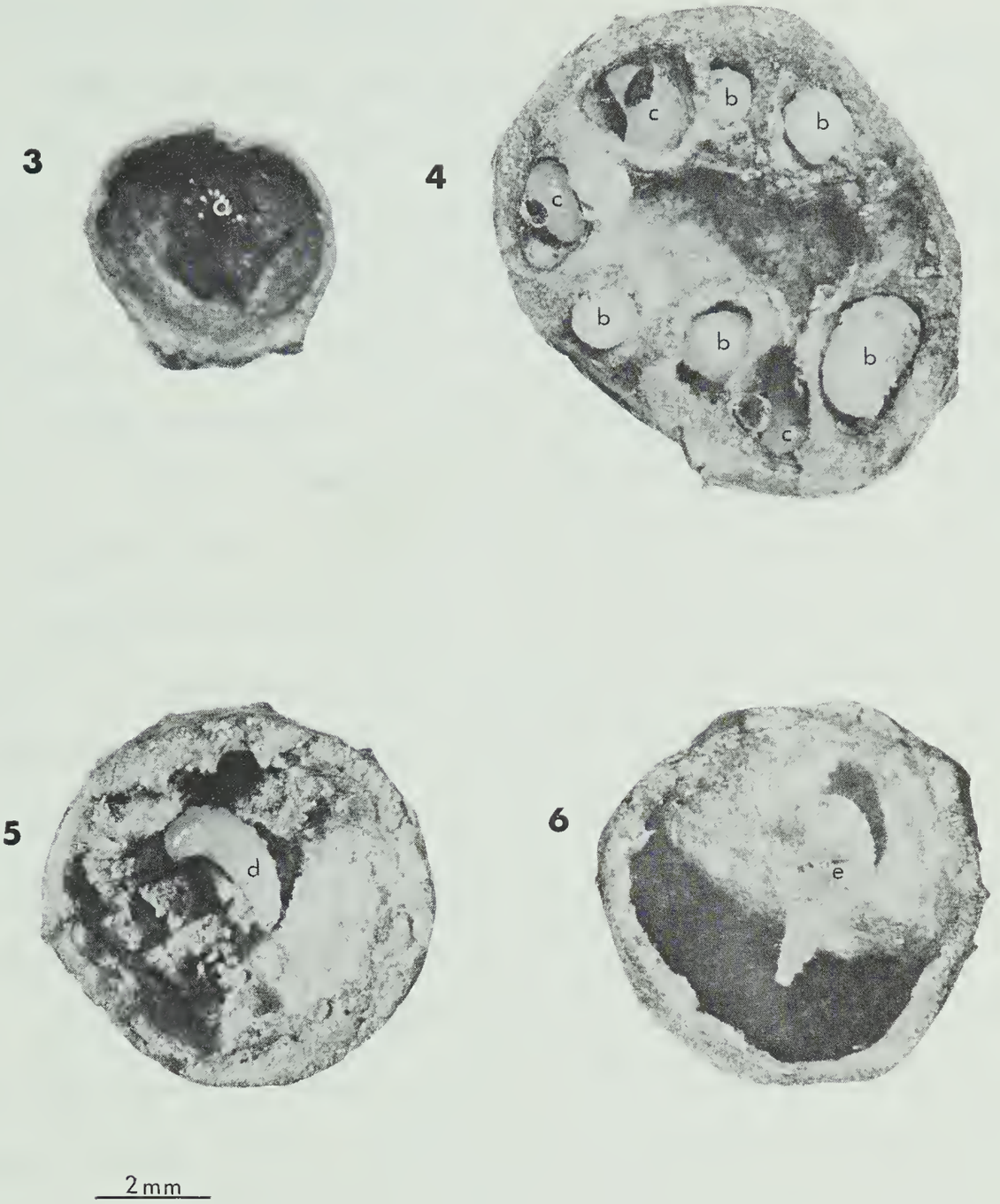
It must be stressed that associating entomophagous species with a particular gall does not give information on host-prey relationships. Great care must be taken in rearing experiments to determine these associations and the present study is one of the few where relationships of the entomophagous species in a gall community have been determined. Before examining the community inter-relationships of the *D. polita* gall, it is first necessary to examine the biology of each inhabitant species.

b) Methods

Galls collected in both 1968 and 1969 were used for studying the biology and life cycles of gall inhabitants. One objective of the 1968 season was to correlate larvae of the inhabitants with their correct adult. When galls and their inhabitants were examined, notes and drawings were made of larval morphology and feeding behavior. The larvae were readily distinguished morphologically (Figs. 7-11) and for three species, *P. pirata*, *E. longavena*, and *G. stigma*, the larvae were readily identified by examining the characteristic damage done to the gall tissues (Figs. 3-6). Only the eggs of *P. pirata*, *E. longavena*, and *G. stigma* are described. When a mature larva was found it was placed in a small pin-mounted gelatin capsule and the capsule stored in a standard insect specimen box. The capsules were checked every 2 days and any developmental changes were noted. The specimen boxes were stored in a field laboratory under nearly ambient temperature and humidity conditions. Specimens emerging in the fall were immediately mounted and labelled as to their rearing capsule. Mandibles of the larvae are structurally dissimilar and were useful characters for identifying species (Figs. 12-17) and associating entomophagous species with their prey. Once the larvae pupated, the mandibles were removed from the larval cast skins and mounted on slides. A correlation between adult, larva, mandibles, and feeding behaviour was obtained in this manner for each species. The remaining larvae were returned to the university and stored at 4°C for 3 months. Once diapause was broken, the larvae were stored at room temperature and a 65% emergence was obtained. Large collections of mature galls were made in the fall of 1968 and were stored in plastic vials. Fall emergence species were collected and the

vials were then overwintered on the ground, subjecting the galls to normal conditions of the subnivean environment. About 200 galls were returned to the university. All gall inhabitants stored in the field were killed when high winds uncovered the box of vials and ambient temperature fell to approximately -55°F. Adults were obtained from the few galls stored at 4°C.

Before the 1969 season began, larva-adult correlations were known for all species except *T. bedeguaris*. One objective of the 1969 season was to obtain data on the biology and life cycles of each inhabitant. Field studies began in the early spring to insure collections of the initial stages in gall development. Field collections were made by randomly walking through areas of *Rosa* and collecting every gall observed. These walks were often more than 1,000 metres in length with the resulting samples being obtained from numerous patches throughout the site. When a gall or gall cluster was found, the entire leaf was picked and placed into an 18 ounce 'Whirl-Pag Bag'. Size of the collection was roughly governed in the field by collecting two bagfuls of galled leaves on each collection date. 27 such random collections were made in the 1969 season. The first 3 collections were small because of the scarcity of galls early in the season but, from June 6 until the end of August, galls were extremely common and no difficulty was found in filling two bags within two hours. Approximately 4,500 galls were collected in this manner. Sizes of 11 of the 27 collections are given in Fig. 20. All galls were returned to the laboratory, measured, dissected, and the contents examined or the galls were fixed in F.A.A. solution for later analysis. By recording the seasonal changes in gall contents and the activities of the larvae found, data were obtained on the biology of



Figs. 3-6. Mature Diplolepis polita galls. 3. Gall inhabited only by Diplolepis polita. 4. Gall modified by Periclistus pirata. 5. Gall modified by Eurytoma longavena. 6. Gall modified by Glyphomerus stigma. (a) Diplolepis polita larva; (b) Periclistus pirata larva; (c) Habrocytus sp. larva; (d) Eurytoma longavena larva; (e) Glyphomerus stigma larva.

all inhabiting species.

c) Life Cycles of Gall Inhabitants

i) *Diplolepis polita* (Ashmead). Little data have been published on the biology of North American *Diplolepis* species and nothing has previously been published on the biology of *Diplolepis polita*. Only 16 adults of *D. polita* were obtained throughout the entire study. 11 adults were obtained from galls stored in the laboratory and 5 from larvae stored in gelatin capsules. Sex ratio of the 16 specimens was .750 (Sex ratio = number of females/total number of individuals). Kinsey (1920a) suggested that in some primitive *Diplolepis* species, normal sexual reproduction may take place, but in the genus as a whole the male is gradually disappearing and parthenogenesis is becoming the sole means of reproduction. Callan (1940) reported that the *Diplolepis* species occurring in Europe appeared to be parthenogenetic and that males were of extreme rarity. He suggested that some species may exhibit geographic parthenogenesis, that is, males may be more numerous in northern latitudes. Kuznetzov-Ugamskij (1930) recorded a *Diplolepis* species from Asia in which the sex ratio was near .500 and in this case parthenogenesis probably does not occur. No adults of *D. polita* were collected by sweeping or trapping in 1968 or 1969, nor were any adults observed ovipositing. It should also be added that no adults of other *Diplolepis* species were collected and it is assumed that field work began too late in the season. The earliest search for adults began May 7, 1969. Yasumatsu and Taketani (1967) observed and described the oviposition of *D. japonica* Walker and estimated the time it took for initial gall growth to occur after oviposition. It is well established (Mani, 1964) that

gall formation is due to larval feeding and presuming proliferation begins soon after the larva commences feeding, the period between oviposition and hatching can be estimated. Yasumatsu and Taketani estimated that the egg stage of *D. japonica* lasts from 7 to 10 days. Callan (1940) experimented with *D. rosae* and found that the first sign of gall formation was from 12 to 36 days after oviposition. The first *D. polita* galls were found May 20, 1969 and it can be estimated that oviposition in this species began in late April (Fig. 18). Only one adult emerged from the 300 mature galls collected in the fall of 1969 (Fig. 19). The eggs of *D. polita* are probably laid in or on the leaf primordia of *R. acicularis* buds (Section IIIBd). Although the eggs of *D. polita* were not examined, they are probably similar to the stalked eggs of other cynipids described by Berland (1951) and Yasumatsu and Taketani (1967). No *D. polita* females were dissected to count eggs. Yasumatsu and Taketani (1967) found that *D. japonica* females contained an average of 331 eggs. *D. polita* females must contain a large number of eggs for although their population is low in the spring, their galls were one of the most common in the study area. When the eggs hatch, the larvae feed on host tissue and initiate formation of the gall (Figs. 30-32). *D. polita* larvae have 12 body segments (Fig. 7), lack setae, and undergo an estimated 5 larval instars. Mandibles of the last instar larva are tridentate (Fig. 12). The larvae grow rapidly and continue feeding on succulent gall cells until the gall matures and hardens. Cosens (1912) stated that cynipid larvae feed only on cell contents and in consequence the cells surrounding the larva soon collapse. The mature gall is hollow and smooth on the inside (Fig. 3). No fecal material is found inside the gall for the larval gut is blind. When the leaf tissue surrounding the gall matures (Section IIIC), the

gall falls to the ground where it is protected throughout the winter by the subnivean environment. *D. polita* overwinters as mature larvae. Laboratory reared specimens had a short pupal stage lasting approximately 10 days. Adults emerge inside the gall, as do nearly all cynipid gall inhabitants and must chew through the gall wall to escape. Laboratory reared specimens lived for about 4 days. Kinsey (1920a) stated that *Diplolepis* adults live for only a few days and must oviposit soon after emergence. Callan (1940) found that males of *D. rosae* appeared before the peak appearance of the females. Kinsey (1920a) also found that adults of most cynipids are killed by sudden changes of temperature or humidity and that adults emerging during inclement weather would not oviposit. Niblett (1947) stated that late frosts are responsible for many casualties and in years when these frosts occur, few galls are to be found.

ii) *Periclistus pirata* (Osten Sacken). The genus *Periclistus* Foerster consists of 7 North American species considered by most authors (Muesebeck et al., 1951) to be restricted to an inquilinous habit in the galls of *Diplolepis* species. Although the exact relationships between *Periclistus* species and the gall formers are not known, it is accepted that the livelihood of *Periclistus* species depends on the presence of *Diplolepis* galls. *Periclistus* larvae are phytophagous and feed on the same gall tissue as do the gall formers. Although *Periclistus* larvae cannot initiate galls, they do cause additional cell proliferation and alter the growth and development of the galls they inhabit (Sections IIIAd and IIIBe). There have been no studies concerned with specificity of *Periclistus* species for *Diplolepis* galls. Fullaway (1911) recorded *P. piceus* Fullaway and *P. californicus* Ashmead from galls of *D. polita*.

Osten Sacken (1863) described *P. pirata* and obtained the specimens from galls of *D. ignota* (O.S.). This present study is the first record of *P. pirata* from the gall of *D. polita*.

P. pirata was an important occupant in the *D. polita* galls of George Lake in 1968 and 1969. 88.5% of the spring initiated galls collected June 6, 1969 contained either eggs or larvae of *P. pirata*. Blair (1944) found that *Periclistus sp.* were present in nearly all the *D. rosae* galls he examined. Although *P. pirata* larvae are phytophagous, in all galls examined their presence indicated that the *D. polita* larva had been destroyed. Although the exact mechanism of this replacement is not known, it has been recorded in other *Diplolepis* galls (Blair, 1945a). Fig. 20 shows that as the eggs of *P. pirata* became more abundant in gall collections, the number of galls containing a live *D. polita* larva was reduced. Because the *D. polita* larva was always dead in galls containing *P. pirata* eggs, oviposition activities of the *P. pirata* females must kill the immature *D. polita*. Once the *D. polita* larva had been killed, it shriveled and became difficult to detect.

P. pirata adults emerged early in the spring probably several days after the *D. polita* adults had emerged and oviposited (Fig. 18). The emergence of *P. pirata* is synchronized with the appearance of the *D. polita* galls. Male *P. pirata* emerge before the females (Fig. 19). The first males were collected in the field May 16, 1969 and the first females May 20, 1969, and the first oviposition was observed May 23, 1969. By June 1, 1969, adults of *P. pirata* were common and 263 were obtained by hand collecting. In the evening the adults rested under the upper leaves of rose and could be easily dropped into collecting vials. Sex ratio of the adults collected in this manner and by spring rearing experiments

was .557. It is interesting that an inquiline cynipid species should have a population composed of equal sexes whereas gall formers have populations dominated by females. Copulation was observed on many occasions both in the field and in the laboratory. Over 300 observations of *P. pirata* ovipositing in immature *D. polita* galls were made (see Frontispiece). If both immature and mature galls were present in a cluster, the immature galls would always be chosen for oviposition first. *P. pirata* must have a lengthy emergence period and although the majority of the population emerges in the spring, adults were found ovipositing in galls up to August 7, 1969. The reappearance of immature galls in July of 1969 (Fig. 24) allowed late emerging females the opportunity for oviposition. The July increase in the number of galls containing *P. pirata* eggs (Fig. 20) is due to the appearance of sucker shoot galls. The mean number of eggs per gall for all collections is given in Table 1. *P. pirata* females would readily oviposit in galls that contained eggs from previous females. The largest number of eggs found in a spring initiated gall was 23 whereas the largest number found in a sucker shoot gall was 16. This could also indicate that more *P. pirata* females were present in the spring than later in the season. The ease with which oviposition could be induced in the laboratory and the observations of oviposition during rainy cool weather, indicated that this species is much more hardy than *Diplolepis* species.

The egg of *P. pirata* is white, of the hymenopteriform type (Clausen, 1940), banana-shaped, and stalked. The stalk, which is as long as the egg, is elastic and has a slight bulge at the distal end. Upon hatching, the larvae distribute themselves around the inner walls of the gall and commence feeding on gall tissues. *P. pirata* larvae feed on the same

cells as *D. polita* larvae and the area in which they feed is always marked by a layer of empty cells (Fig. 37). As the larvae continue feeding, gall tissue surrounds each individual in an inner chamber. Blair (1945b) found that *Synergus reinhardi* Mayr (Cynipidae) modified the galls of *Cynips kollari* Hartig (Cynipidae) in a similar manner. Galls containing *P. pirata* chambers appear polythalamous and the cavities, once containing a single *D. polita* larva, are nearly obliterated (Fig. 4). *P. pirata* larvae (Fig. 8) with their tridentate mandibles (Fig. 13) are easily distinguished from the larva and mandibles of *D. polita*. *P. pirata* larvae are not as active as the *D. polita* larvae and do not thrash as violently when disturbed. *P. pirata* inhabited galls fall to the ground and receive the same protection in the subnivean environment as do *D. polita* larvae. The seasonal change in the percentage of galls with larvae and the mean number of larvae per gall is shown in Table 1. The pupal stage of laboratory reared individuals lasted about 9 days. On May 17, 1969 I found 4 galls that had caught on a branch and overwintered 3 inches above the ground. Two of the galls contained *P. pirata* larvae and each larva was placed into a gelatin capsule. All larvae pupated and adults emerged by May 21, 1969. This indicated that the pupal stage is much shorter for field reared specimens than laboratory reared specimens. Many of the galls collected in the fall of 1969 and overwintered in the laboratory at 4°C and then moved to 25°C, were dissected 4 months after emergence had ceased. About 3% of the *P. pirata* inner chambers contained live larvae. Under normal conditions these larvae may have been destined for emergence later in the season or their presence may indicate that a small percentage of the *P. pirata* population remains in the larval stage throughout the season

Table 1

Incidence of *Periclistus pirata* eggs and larvae in the galls of *Diplolepis polita*. George Lake, Alberta. 1969.

Date	Sample Size	% of galls with eggs	Mean no. of eggs per gall (S.D.)*		% of galls with larvae	Mean no. of larvae per gall (S.D.)*	
20-V	4	0	0	0	0	0	0
25-V	55	38.1	6.2	(3.9)	0	0	0
28-V	54	83.5	10.1	(6.8)	0	0	0
6-VI	166	43.6	5.4	(4.8)	71.0	6.9	(5.5)
12-VI	156	13.0	3.0	(1.8)	62.3	5.7	(3.7)
20-VI	176	8.1	2.5	(1.5)	37.0	4.1	(3.6)
27-VI	127	2.1	-	-	35.4	4.2	(3.8)
5-VII	119	0	0	0	25.2	3.6	(3.3)
14-VII (spring)	156	0	0	0	20.0	3.7	(2.9)
14-VII (sucker)	21	80.9	5.0	(4.1)	9.5	5.0	(4.1)
23-VII (spring)	190	0	0	0	17.2	3.9	(3.6)
23-VII (sucker)	106	9.4	4.9	(4.1)	50.0	5.2	(4.2)
22-VIII	275	0	0	0	8.1	3.5	(3.2)

*means are calculated exclusive of galls without eggs or larvae

spring = galls initiated in the spring only

sucker = galls initiated on sucker shoots only

and emerges the following year.

P. pirata larvae form the main food source for the entomophagous species associated with the gall and the combined activities of these predators reduce the *P. pirata* population (Fig. 20) (Section IIBc).

iii) *Eurytoma longavena* Bugbee. Eurytomids are one of the most common entomophagous groups associated with *Diplolepis* galls. Bugbee (1967) listed 82 species of North American *Eurytoma* and stated that 33 species attack Hymenoptera. He stated that at least 12 species are known to be phytophagous and listed one species, *E. pachyneuron* Girault, suspected of being both parasitic and phytophagous. Peck (1963) presented a comprehensive bibliography for 72 North American species. Although most gall inhabiting eurytomids are considered parasitic, the lack of detailed life cycle studies hinders such generalizations. Bugbee (1951) discussed 12 species known from *Diplolepis* galls and warned that knowing the associated gall gives little data on actual host relationships. Also in this paper he discussed phylogeny of the *Eurytoma* species associated with *Diplolepis* galls. He suggested that in most cases *Eurytoma* are restricted to a single species of gall former, but also listed several species known from more than one gall and suggested that further studies will reveal more complex relationships. He pointed out that some species may attack inquilines and other gall inhabitants besides the gall former. Bugbee (1951) also stated that no complete life-histories have been worked out for any of the Nearctic species associated with *Diplolepis* galls.

E. longavena was the most common and influential entomophagous occupant in the 1968 and 1969 *D. polita* gall community (Section IIBc). This species was described by Bugbee in 1951 and was found inhabiting

D. bicolor galls growing on an undetermined species of *Rosa*. *E. longavena* is known only from its type locality of Terrace, British Columbia and according to Bugbee (pers. comm.) nothing is known of its biology. Three species of *Eurytoma* have previously been associated with *D. polita* galls (Bugbee, 1951); these are *E. flavicrurensa* Bugbee, *E. incerta* Fullaway, and *E. terrea* Bugbee. *E. longavena* has not been previously recorded from the *D. polita* gall.

Larvae of *E. longavena* were found in 17% of the mature galls collected August 17-23, 1968 and in 32% of the galls collected August 22, 1969 (Fig. 20). Most of the empty galls found in 1968 and 1969 were also a result of *E. longavena* activities. Gall collections described in Section IIAb were used in tabulating incidence of *E. longavena* eggs, larvae, and pupae in the galls of the 1969 season (Table 2). *E. longavena* has two generations per year, although only a small percentage of the total population is derived from the second generation. From a large collection of 1969 spring initiated galls, 12.3% of the *E. longavena* population emerged the same season and the remainder emerged the following spring. Adults that emerged in the fall of the same season were able to oviposit in sucker shoot galls. The *E. longavena* population found in sucker shoot galls emerge the following spring. Clausen (1940) stated that the number of generations of *Eurytoma* per year is dependent upon the hosts attacked and mentioned that *E. monemae* Ruschka may have three generations per year.

Bugbee (1951) stated that the sex ratios for several species he studied were approximately equal although females are usually more numerous. A total of 423 *E. longavena* adults were obtained throughout this study and the sex ratio was .912. The fall populations of

E. longavena consisted of females only and the sex ratio of all individuals collected, exclusive of fall emergents, was .892. Niblett (1947) found that a small percentage of the *E. rosae* Nees population emerged in the first year and that the sexes were in equal numbers. *E. longavena* females emerged late in the season from 5% of the mature galls collected in 1968 and from 7% of the mature galls in 1969.

Fig. 19 indicates that *E. longavena* adults emerge about the same time as *P. pirata* and are probably present when the first *D. polita* galls appear. The first eggs were found in galls collected May 25, 1969, although the earliest oviposition was observed June 5, 1969. A total of 53 ovipositions were observed in the 1969 season (Fig. 18). Spring adults emerge over a long period of time as indicated in Fig. 19. Although the last oviposition was observed August 9, 1969, such females could have come from spring or fall populations. This extended activity period is shown by the presence of eggs in sucker shoot galls (Table 2). These eggs could have been deposited by either late spring emergents or fall emergents. The mean number of eggs laid per gall is also shown in Table 2. Dates without data were due to difficulties in locating eggs amongst *P. pirata* chambers and uneaten gall residues. As with *P. pirata*, *E. longavena* would readily oviposit in galls containing eggs from previous females.

E. longavena eggs are similar in appearance to other *Eurytoma* eggs as described by Clausen (1940) and Phillips (1927). They are brown, oval-shaped, and have a small curled stalk at one end. The stalk is about one-third as long as the egg. The eggs are white immediately after oviposition but turn brown within 24 hours. Several *E. longavena* females were dissected and all contained 6 eggs or less. The largest number of

eggs found in a spring initiated gall was 11 and the largest number in a sucker shoot gall was 4. *E. longavena* eggs were found only in immature galls containing eggs or larvae of *P. pirata*. No eggs were found in galls containing a *D. polita* larva, indicating that the females can detect gall contents. Eggs were deposited along the inner walls of the gall and upon hatching the larvae immediately began feeding on the eggs or larvae of *P. pirata* or on any gall inhabitants they subsequently encountered. Because *P. pirata* was the most abundant species in the gall community (Section IIBc), it was the chief host of *E. longavena*. I observed several *E. longavena* larvae feeding even before they were completely free of their egg shells. Later in the season *E. longavena* larvae were also found consuming immature larvae of *G. stigma*, *T. bedeguaris*, and *Habrocytus sp.* *E. longavena* are also cannibalistic and although most galls attacked by this species contained several eggs (Table 2), only one larva usually survived. 94% of the galls containing *E. longavena* produced a single adult. Galls producing two adults were large and contained sufficient food to support more than one larva. Caltagirone (1964) stated that when more than two *Eurytoma sp.* eggs were present in the *Pontania* gall he studied, the larvae that hatched first killed the remaining eggs.

E. longavena larvae are both entomophagous and phytophagous but they must feed on insect tissue before they feed on plant tissue. This is shown by specimens that do not survive if hatched inside galls with completed *P. pirata* chambers. *E. longavena* larvae must consume free host material before they are capable of chewing through chamber walls. Once the *E. longavena* larvae have reached a certain stage in their development, they are capable of feeding on either plant tissues or insect tissues

found inside the *P. pirata* chambers. Once the *P. pirata* larvae are enclosed by gall tissues, the *E. longavena* larvae must chew through chamber walls if more insect tissue is required. If the combined feeding activities of several *E. longavena* larvae consume all insect host material before they are capable of phytophagous feeding, all will perish and an empty gall results. Most galls contained sufficient immature *P. pirata* to supply the *E. longavena* with food and also allow for some *P. pirata* to escape and form chambers. It is pertinent that the hosts are not killed at the time of oviposition, for the presence of *P. pirata* larvae provide the *E. longavena* larvae with access to succulent parenchyma cells and to other entomophagous species attracted to the chambers. Because the *E. longavena* larvae feed externally and require several hosts, I consider them predators rather than ectoparasites. Blair (1944) suggested the same for *E. rosae* Nees found in the galls of *D. rosae* L., but received opposition from Niblett (1947) and Askew (1961). Moser (1965), Caltagirone (1964), and Malyshev (1968) reported that the gall inhabiting *Eurytoma* species they studied stung and paralysed the hosts at the time of oviposition.

When the *E. longavena* larvae chew from chamber to chamber, uneaten plant residues accumulate inside the gall and this condition is characteristic of *Eurytoma* damage (Fig. 5). Although the presence of this residue suggests that the larvae tear through chamber walls, I observed many specimens ingesting plant cells confirming the species is phytophagous. Varley (1937) recorded the same behavior for the larvae of *E. robusta* Mayr. Blair (1945a) stated that the larvae of *E. rosae* feed on *Periclistus* larvae and chew into gall tissues but did not record a phytophagous habit. Malyshev (1968) listed several other eurytomids

Table 2

Incidence of *Eurytoma longavena* eggs, larvae, and pupae in the galls of *Diplolepis polita*. George Lake, Alberta. 1969.

Date	Sample size	% of galls with eggs (hatched & unhatched)	Mean no. of eggs per gall (S.D.)*		% of eggs hatched	% of galls with larvae	% of galls with pupae
20-V	4	0	0		0	0	0
25-V	55	3.4	1	(0)	0	0	0
28-V	54	33.8	1.1	(0.4)	0	0	0
6-VI	166	78.3	2.1	(1.3)	38.7	16.0	0
12-VI	156	87.1	2.7	(1.3)	48.0	44.8	0
20-VI	176	89.2	3.1	(2.0)	61.0	52.8	0
27-VI	127	85.8	2.2	(1.3)	80.4	51.1	0
5-VII	119	90.7	2.4	(1.6)	92.0	63.8	0
14-VII (spring)	156	—[1]	—[1]	—[1]	—[1]	47.5	5.0
14-VII (sucker)	21	26.6	2.5	(1.6)	0	0	0
23-VII (spring)	190	—[1]	—[1]	—[1]	100[2]	38.2	0
23-VII (sucker)	106	81.1	2.1	(1.2)	44.0	41.5	0
22-VIII	275	—[1]	—[1]	—[1]	100[2]	32.1	0

*means are calculated exclusive of galls without eggs

[1]no data available

[2]estimate

spring = galls initiated in the spring only

sucker = galls initiated on sucker shoots only

that initially feed on eggs and host larvae and then feed on gall tissues. It appears that once a *E. longavena* larva consumes a certain amount of entomophagous material, it is capable of continued development on gall tissues. Phillips (1927) in his study of *E. parva* (Girault), suggested that this species, similar to *E. longavena*, is gradually breaking away from the entomophagous habit and is becoming phytophagous. Blair (1945a) suggested the same for *E. rosae*.

Mature *E. longavena* larvae are recognized by their distinct segmentation, abdominal protrusions, and anterior sensory setae (Fig. 9). The larval mandibles (Fig. 14) are heavily scleritized, triangular in outline, and each has one large denticle on the inner margin. The larvae do not void excrement until they are mature, presumably as a precaution against food contamination. *E. longavena* larvae overwinter inside the gall and pupate the following spring. The pupal stage of laboratory reared specimens lasted about 12 days.

iv) *Glyphomerus stigma* (Fabricius). Genus *Glyphomerus* is monobasic containing the single species *G. stigma*. This species, described in 1793 by Fabricius, has a Holarctic distribution and is known mainly as an ectoparasite of gall inhabitants. Viereck (1916) recorded it from the *D. rosae* gall and Hoffmeyer (1930) recorded it from the *D. polita* gall. Peck (1963) presented a bibliography of North American records and Fulmek (1968) listed it as associated with 6 of the 7 European species of *Diplolepis*. *G. stigma* is therefore not host specific for it has been recorded from 3 Nearctic galls (Peck, 1963) and 9 Palearctic galls (Fulmek, 1968). Blair (1945a) found the species attacking *Periclistus brandtii* Er. in the galls of *D. rosae*. Other than these few host records, nothing to my knowledge is known of its biology.

The same gall collections mentioned previously (Section 11Ab) were used in tabulating the incidence of *G. stigma* eggs and larvae in the *D. polita* galls collected in 1969 (Table 3). Larvae of *G. stigma* were found in 21% of the mature galls collected August 17-23, 1968 and in 12.5% of the mature galls collected August 22, 1969 (Fig. 20). *G. stigma* at George Lake is univoltine, although Niblett (1947) found that a few adults associated with British galls, emerged in the fall of the first season. Fig. 19 indicates that the George Lake males emerge before females and this was confirmed by field collections. Females are rapid fliers and unless they are found with their ovipositors inserted deep into a gall, they are exceedingly difficult to capture. I obtained a total of 139 adults from gall emergence studies and the sex ratio was .561. *G. stigma* has a lengthy period of emergence as indicated by the 42 oviposition observations shown in Fig. 18 and the presence of eggs in galls collected in early season and sucker shoot galls (Table 3). Niblett (1947) found that July and August was the normal emergence time for British populations associated with *D. rosae* galls. I recorded the first oviposition May 23, 1969 although the first eggs were not found until June 6, 1969 (Table 3). Laboratory emergence studies (Fig. 19) indicated that the peak emergence occurs after that of *P. pirata* and *E. longavena*.

G. stigma eggs are white to transparent and are banana-shaped with one end slightly thicker than the other. The thicker end also has a small knob on the tip. The long ovipositor of the adult enables it to oviposit in large, thicker walled galls unavailable to *E. longavena*. The eggs are laid on the inside surface of the gall cavity. Once the larvae hatch, the egg shells are almost impossible to detect and therefore

Table 3 includes only unhatched eggs. Some of the unhatched eggs may have been missed and this could be one explanation for the sudden increase of galls containing larvae in the August 22, 1969 collection (Table 3). 80% of the 1969 attacked galls contained a single egg and the remaining contained two eggs. The larvae are cannibalistic and the first hatched consumes other eggs present, with the result that no more than one *G. stigma* larva was ever found per gall. Because this species consumes all inhabitants of the *D. polita* galls in which they occur, it plays an important role in the gall community (Section IIBc). *G. stigma* larvae were found preying upon the larvae of *D. polita*, *P. pirata*, *E. longavena*, *T. bedeguaris* and *Habrocytus sp.*, with the most important host being *P. pirata*. Chamber wall tissue was consumed when the attacked gall contained *P. pirata*, indicating that the species is phytophagous as well as entomophagous. Larvae of *E. longavena* and *Habrocytus sp.* were consumed if they were inside *P. pirata* chambers when attacked by a *G. stigma* larva. Because *G. stigma* larvae devour more than one host, I consider them predators rather than parasites. Galls attacked by *G. stigma* larvae have their interiors hollowed and are similar in appearance to normal galls containing a *D. polita* larva (Fig. 6). The larvae consume most of the gall nutritive zone cells and as a result the damaged gall has an interior lined with several layers of cell particles (Fig. 34).

Blair (1945a) gave a brief description of the *G. stigma* larva. The mature larva is white, tapers towards the tail and is clothed with long soft hairs (Fig. 10). The head is cordiform and has two deep, elongated fossae that turn dark brown as the larva matures. Mandibles of the mature larva are slender and curved with a denticle on the inner side some distance before the apex (Fig. 15). Larvae overwinter inside the

Table 3

Incidence of *Glyphomerus stigma* eggs and larvae in the galls of *Diplolepis polita*. George Lake, Alberta. 1969.

Date	Sample Size	% of galls with eggs (unhatched)	% of galls with larva
20-V	4	0	0
25-V	55	0	0
28-V	54	0	0
6-VI	166	9.0	0
12-VI	156	11.5	0
20-VI	176	22.1	0
27-VI	127	13.0	1.0
5-VII	119	3.8	3.4
14-VII (spring)	156	0	4.5
14-VII (sucker)	21	5.0	0
23-VII (spring)	190	0	5.4
23-VII (sucker)	106	5.6	0
22-VIII	275	0	12.5

spring = galls initiated in the spring only

sucker = galls initiated on sucker shoots only

gall and pupate the following season. Pupal stage of laboratory reared specimens lasted about 20 days.

v) *Torymus bedeguaris*. The genus *Torymus* includes both phytophagous as well as entomophagous species with the entomophagous species mainly attacking gall makers and gall inhabitants. According to Huber (1927), genus *Torymus* in North America is known to include 40 species that attack immature stages of Cynipoidea. Of the 106 Nearctic Torymids listed by Peck (1963), 7 are recorded from *Diplolepis* galls. Fulmek (1968) listed 103 European species associated with insect galls and recorded 6 of the 7 European *Diplolepis* as hosts. He recorded one *Diplolepis* species known as the host for 10 *Torymus* species. *T. bedeguaris*, a Holarctic species, was found associated with George Lake *D. polita* galls but it was the least common species in the community. Peck (1963) listed three species of *Diplolepis* known as hosts of *T. bedeguaris* and Fulmek (1968) listed 9 European gall formers as hosts. *T. bedeguaris* has not been previously recorded from *D. polita* galls.

Only 132 *T. bedeguaris* adults were obtained in the two years and the sex ratio for the series was .404. Clausen (1940) stated that there is a preponderance of females for all species in which sex ratios are known. The abundance of males in the present study may only be the result of a small series. 39 adults emerged in the fall of 1968 from galls collected that spring and the sex ratio of these specimens was .435. No adults emerged in the fall of 1969 from galls collected that season, although 44 were obtained once diapause was broken. Sex ratio of these specimens was .388. Only 4 adults emerged from the 300 galls used in the spring emergence study (Fig. 19). This figure indicates that the species emerges late in the season and this was substantiated by field observations.

Although it is strange that some adults emerged in the fall of 1968 and none emerged in the fall of 1969, the fact that so few specimens were obtained makes it difficult to discuss population trends with any degree of certainty. *T. bedeguaris* may have two generations per year if subjected to proper conditions. Their population may have been high in the spring of 1968 and suitable conditions allowed many adults to emerge in the fall. Varley (1941) stated that temperature influenced the fall emergence of *T. cyanimus* Boh., an ectoparasite of *Urophora jaceana* Hering (Family Tephritidae). All *T. bedeguaris* that emerged in the fall of 1968 did so in late August or early September, a date when few oviposition sites were available. These late season emergences and lack of oviposition sites may have resulted in a slight population crash and thus a scarcity of specimens in 1969. Varley (1937) stated that the larvae of *T. cyanimus* attacked the full grown host larvae in August. He found some adults emerging in the fall, but the majority passed the winter in the larval stage and emerged the following spring. In 1947 he reported that although most *T. cyanimus* adults emerged in May, no eggs or larvae were found until August. As an explanation, he suggested that *T. cyanimus* may have an alternative host or the adults may wait from May until August before the eggs are matured and laid. Moser (1965) reported that *T. vesiculus* Moser, an ectoparasite of *Pachypsylla celtidivesicula* Riley (Family Psyllidae, Order Homoptera), has two generations per year with some of the first and all of the second generation overwintering as mature larvae inside the gall.

Three *T. bedeguaris* were observed ovipositing in sucker shoot galls in 1968 and one was observed in 1969. 8 other females were collected in the field in July and August of 1969, indicating that the species is

active later in the season than other members of the community (Fig. 18). Laboratory emergence studies (Fig. 19) also indicated that this species appears later in the season. *T. bedeguaris* adults were as difficult to capture as adults of *G. stigma*.

No *T. bedeguaris* eggs were identified in any of the 1968 or 1969 gall collections, although they may have been confused with *G. stigma* eggs. Only 4 larvae were found in the August 22, 1969 collection (Fig. 20) and two of these were reared to adults. 10 adults were obtained from rearing larvae in gelatin capsules. 8 of these were obtained as first or second instar larvae found attached to dead mature larvae of either *D. polita*, *P. pirata*, *G. stigma*, or *E. longavena*. The occurrence of first and second instar larvae late in August indicated that the species must be capable of rapid maturity. Only 5 mature larvae were ever found and 2 of these were reared to adults. From these few observations it appeared that the female kills the host at oviposition and lays only a single egg. Varley (1947) reported that *T. cyanimus* often laid eggs in groups and although several larvae may be found feeding on the same host, only one larva matured. Hosts of *T. bedeguaris* are completely consumed leaving only an empty cast skin. Because *T. bedeguaris* matures on a single host, I consider it an ectoparasite. An illustration of the larva was not made for this species, although a brief description can be given. It is slightly smaller than the *G. stigma* larva, but is not tapered, nor does it have the sunken fossae as *G. stigma*. Its body surface has some long setae, but it is not as densely clothed as *G. stigma*. The mandibles (Fig. 16) are narrow and acute without denticles and are difficult to locate in the larval cast skins.

vi) *Habrocytus sp.* (Indet.). Family Pteromalidae is one of the most

common of the Chalcidoidea and many of the species are known to attack larvae of Hymenoptera. The biology of most species remains unknown and Peck (pers. comm.) stated that the entire genus *Habrocytus* requires revision. Specific characters have yet to be worked out. Peck (1963) listed 31 species of *Habrocytus* and recorded 3 associated with *Diplolepis* galls. Fulmek (1968) recorded 15 European species and listed 4 associated with *Diplolepis* galls. The present study is the first record of a *Habrocytus* species from the *D. polita* gall. This species has not been determined.

Habrocytus sp. larvae were only found attacking larvae of *P. pirata*, although I suspect they attack *D. polita* larvae along with other inhabitants. *P. pirata* chambers are probably completed and the larvae matured before *Habrocytus sp.* oviposits. Varley (1937) suggested that *H. trypetae* Thoms. was not specific in its choice of hosts and would attack other parasites encountered. Blair (1944) found that *H. bedeguaris* Thoms. attacked full grown larvae and pupae of *Diplolepis* and *Periclistus* and that cannibalism often occurred. No eggs of *Habrocytus sp.* were found and the first larvae were observed July 5, 1969 (Table 4) crawling over paralyzed *P. pirata* larvae. Only a single larva was found per host and the number of larvae per gall is dependent upon the number of *P. pirata* larvae present (Table 4). The largest number of *Habrocytus sp.* larvae found in one gall was 11. Superparasitism, as Varley (1947) recorded for *H. trypetae*, was not observed, although if several eggs had been laid per host, the first hatched could easily have consumed other eggs or larvae present. Urbahns (1916) in his study of *H. medicaginis* Gahan also found only a single larva was able to develop per host. The larvae of *Habrocytus sp.* are therefore ectoparasitic. They destroy their hosts

quickly and only a round, black, pellet remains. This pellet is readily visible in dissected galls (Fig. 4) and was used as the species indicator. Urbahns (1916) stated that the larva of *H. medicaginis* Gahan can become fully developed in 6 days after its first meal. *Habrocytus sp.* overwintered in the larval stage inside the gall.

Approximately 300 adults were obtained in this study. The sex ratio of these specimens was not determined for the adults are difficult to sex. Clausen (1940) stated that one *Habrocytus* species is known to have a preponderance of females. *Habrocytus sp.* adults emerged late in the season and were the last species in the *D. polita* gall community to emerge (Fig. 19). 42 observations of oviposition were made, the earliest was June 22, 1969 and the last was August 20, 1969 (Fig. 18). Only two adults were observed ovipositing in sucker shoot galls. Sucker shoot galls were not readily attacked by *Habrocytus sp.* because few *P. pirata* larvae were able to form inner chambers.

Habrocytus sp. is univoltine and the adults emerge the following season. Niblett (1947) found that a few adults of *H. bedeguaris* emerged in the fall of the first year, but the majority emerged in July and August of the second year. Several mature galls exposed to 4°C for 3 months were dissected 4 months after gall inhabitants had stopped emerging. Live *Habrocytus sp.* larvae were found in a few of the *P. pirata* chambers indicating that the species may be capable of an extended larval stage and emergence two seasons later. Many *Habrocytus sp.* larvae are probably consumed by larvae of *E. longavena, G. stigma,* and *T. bedeguaris* (Section IIBc). The decrease in the number of *Habrocytus sp.* larvae per gall (Table 4) is partly due to the activities of these predators. The inclusion of sucker shoot galls, which contain few if any *Habrocytus sp.* larvae,

Table 4

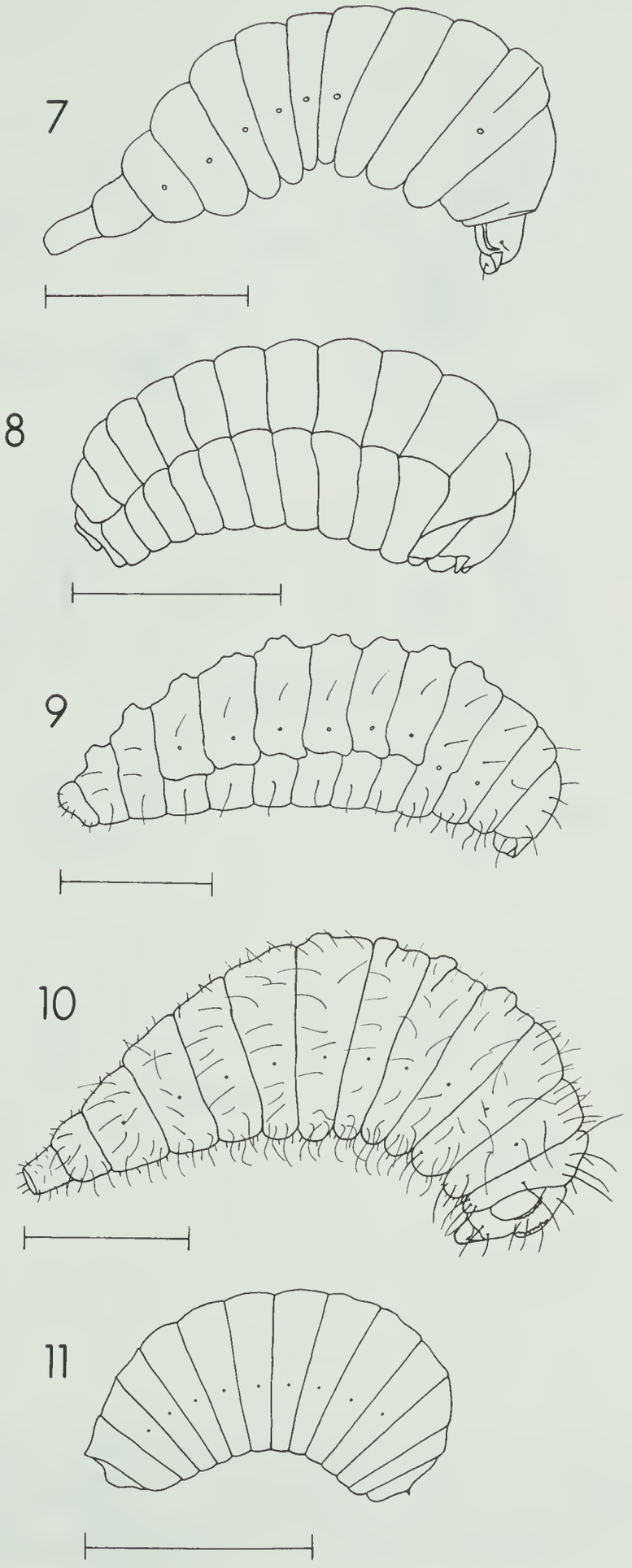
Incidence of *Habrocytus sp.* larvae in the galls of *Diplolepis polita.* George Lake,Alberta. 1969.

Date	Sample size	% of galls with larvae	Mean no. of larvae per gall (S.D.)*
20-V	4	0	0
25-V	55	0	0
28-V	54	0	0
6-VI	166	0	0
12-VI	156	0	0
20-VI	176	0	0
27-VI	127	0	0
5-VII	119	1.0	1.0 (0)
14-VII (spring)	156	5.0	1.0 (0.3)
14-VII (sucker)	21	0	0
23-VII (spring)	190	23.0	2.7 (2.4)
23-VII (sucker)	106	0	0
22-VIII	275	8.1	3.0 (1.9)

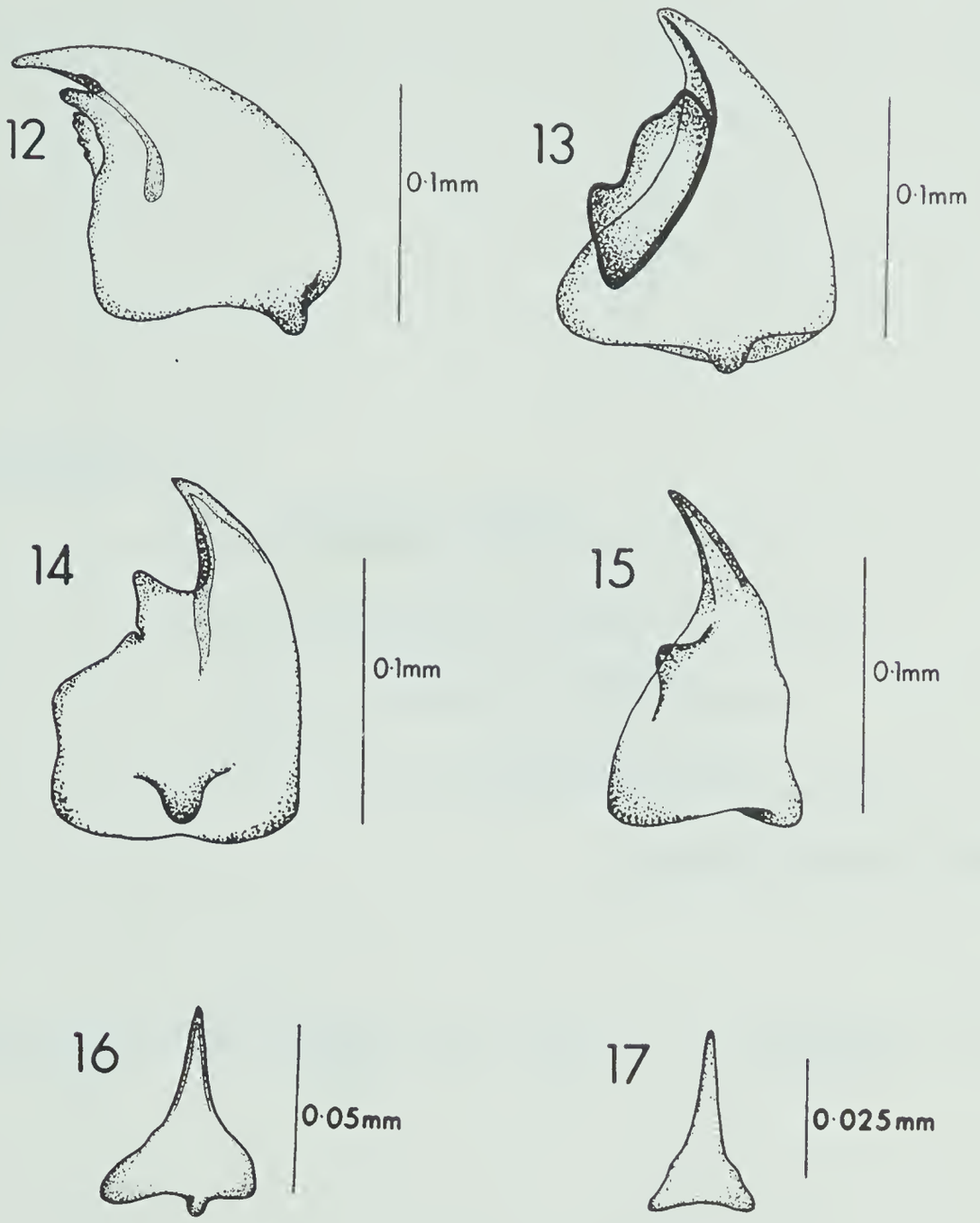
*means are calculated exclusive of galls without larvae

spring = galls initiated in the spring only

sucker = galls initiated on sucker shoots only



Figs. 7-11. Mature larvae of Diplolepis polita gall inhabitants. 7. Diplolepis polita. 8. Periclistus pirata. 9. Eurytoma longavena. 10. Glyphomerus stigma. 11. Habrocytus sp. Accompanying scale lines equal 1.0 mm.



Figs. 12-17. Mandibles of mature larvae found in galls of Diplolepis polita. 12. Diplolepis polita. 13. Periclistus pirata. 14. Eurytoma longavena. 15. Glyphomerus stigma 16. Torymus bedeguaris. 17. Habrocytus sp.

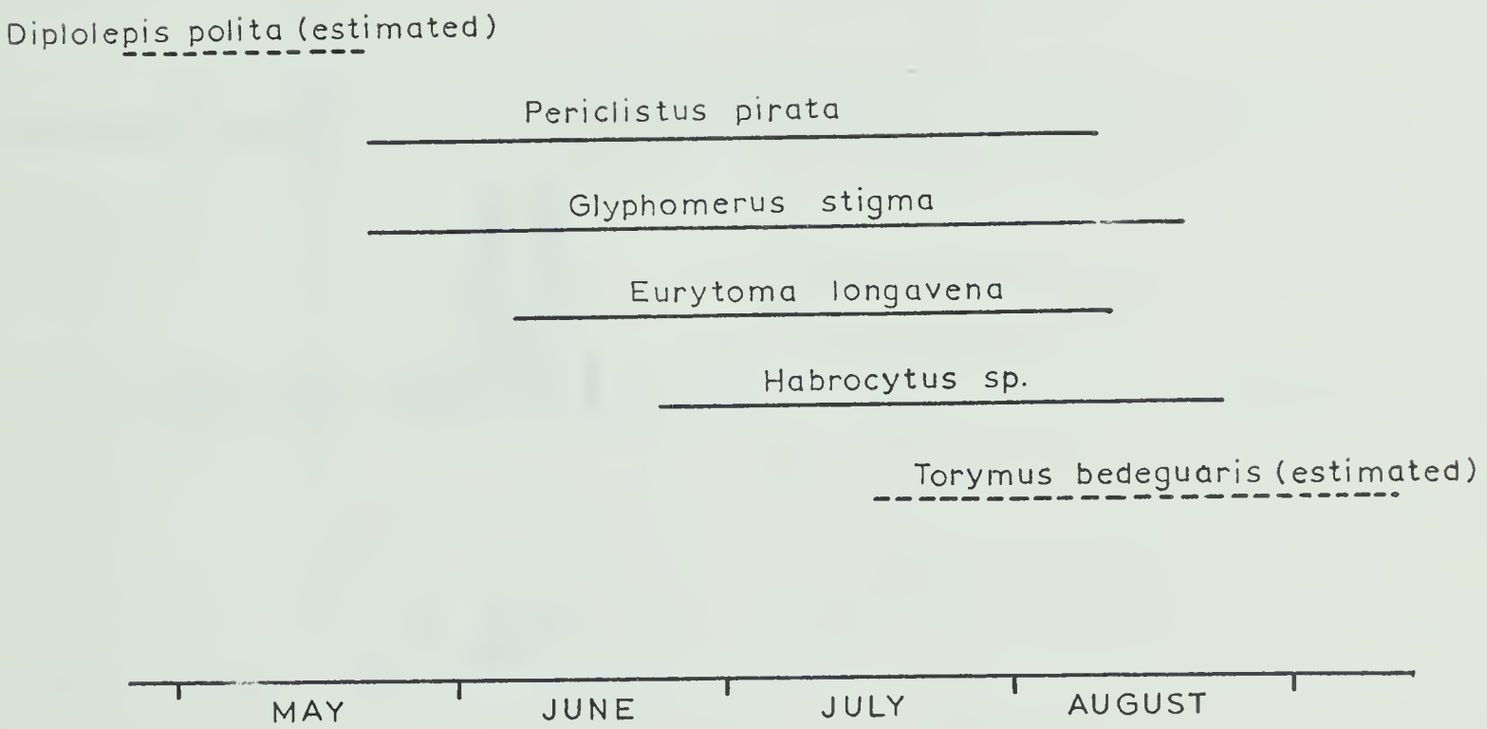


Fig. 18. Oviposition periods recorded for species associated with Diplolepis polita galls. 1969. George Lake, Alberta.

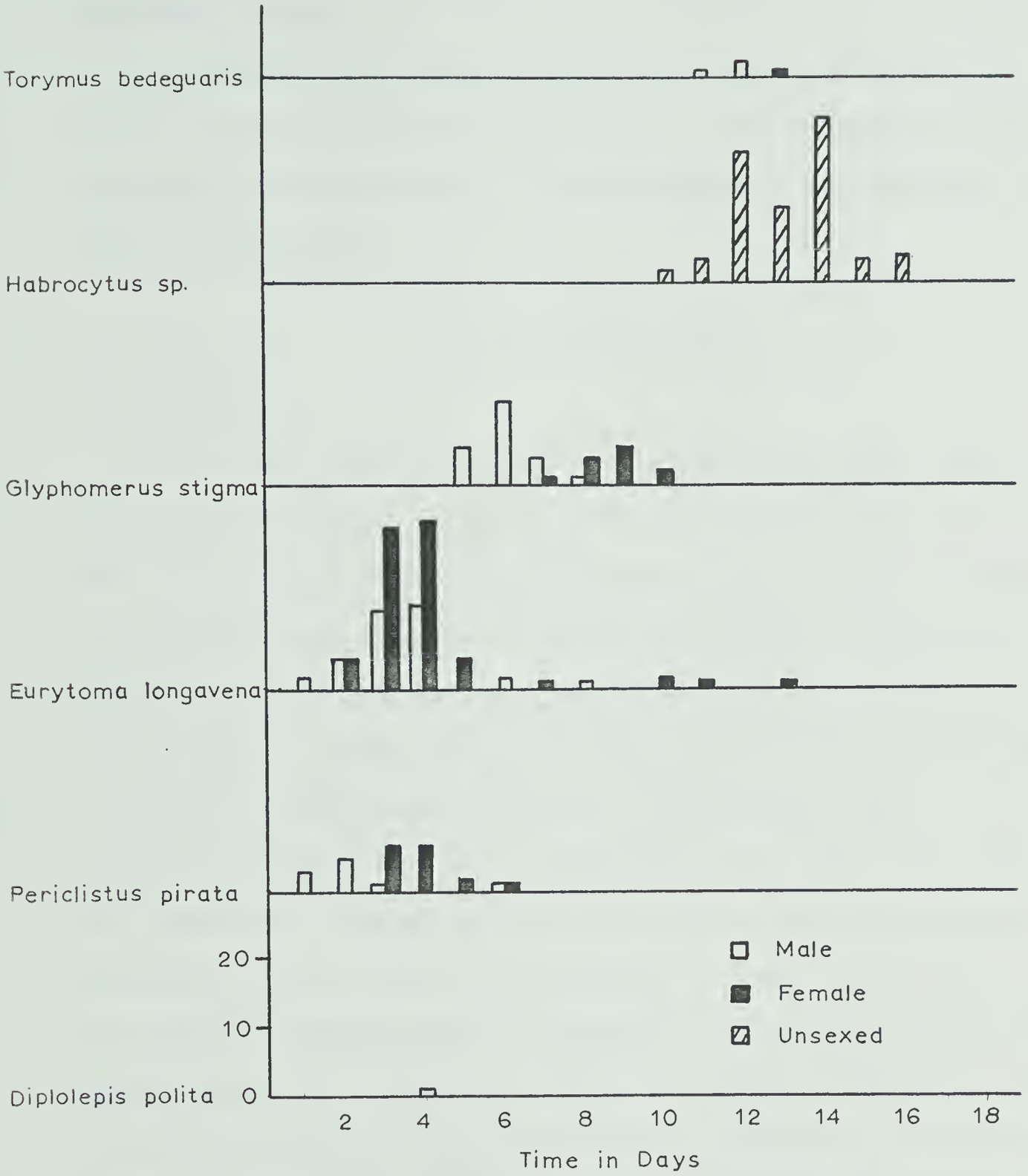


Fig. 19. Spring emergence from 300 Diplolepis polita galls stored under laboratory conditions. Galls collected at George Lake, Alberta. 1969.

in the August 22, 1969 collection, also decreased the percentage of galls with larvae.

The mature grublike *Habrocytus sp.* larva lacks distinguishing features and has weak segmentation (Fig. 11). The integument is smooth and sensory setae are reduced. The tiny mandibles are simple and lack denticles (Fig. 17).

B) Community Studies

a) Introduction

Mani (1964) briefly introduced the study of plant gall communities and listed 33 different roles into which gall inhabitants can be classified. He stated that the predator-parasite complex of galls is often considerably larger than that of inquilines and while some galls lack inquilines few, if any, are free from entomophagous inhabitants. The classic paper on this subject is by Varley (1947) in which he discussed factors controlling population density of the knapweed gall-fly. The 5 species associated with the *D. polita* gall form a small, but rather complex community. Although there are many factors regulating the gall former population, such as weather and availability of oviposition sites, it is the objective of this section to examine the roles played by each member species in the gall community. Because each species appeared at a different time throughout the season, there was community succession and climax. As Mani (1964) stated, climax of gall community succession is marked by a dominance of entomophagous species. Climax in the *D. polita* gall community occurred when the galls matured and fell to the ground, for once this stage was reached, oviposition and larval feeding activities ceased. Timing of emergence and oviposition is critical for all species

of the community because early or late emergence reduces their efficiency as regulating agents. The influence of sucker shoot galls on the total community was regulated by extended emergence periods of some member species.

b) Methods

Nearly all data on the *D. polita* gall community was obtained in the 1969 season. Galls collected in 1968 were mainly used for obtaining data on the biology of each member species. 11 of the 27 random collections made in 1969 (Section IIAb) were used in the community study. Because nearly all galls had matured by August 8, 1969 (Fig. 40), only one large August collection was used.

The number of empty galls in each collection increased (Fig. 21) as the season advanced. In this study, an empty gall is defined as one which does not contain a live inhabitant and therefore cannot contribute to the community. Galls from which *E. longavena* of *T. bedeguaris* adults emerged late in the season, had a tiny emergence hole and were not considered empty (Fig. 21).

c) Results and Discussion

D. polita is the central species in the gall community for it causes gall formation and without the gall none of the subsequent species could exist. When the galls first appeared in the spring, *D. polita* predominated. The first three collections in 1969 contained only larvae of *D. polita* (Figs. 20 and 22). The *D. polita* larval population decreased once *P. pirata* eggs appeared suggesting that they were killed by oviposition activities of *P. pirata* females (Section IIAcii). By May 28, only 18.5% of the galls contained a live *D. polita* larva, although only the eggs of

P. pirata and *E. longavena* were present in the remaining galls (Fig. 20). If *E. longavena* occurred in galls without *P. pirata*, it would undoubtedly devour the *D. polita* larva resulting in a further decrease in the *D. polita* population. The largest population of *P. pirata* larvae occurred early in the season (Fig. 22) and because they formed the main food source of the entomophagous species, their dominance began to decline. *E. longavena* had the greatest influence on the *P. pirata* population and the number of galls containing the former species had risen rapidly by June 20 (Fig. 20). Varley (1947) found that *E. curta* Walker was chiefly responsible for controlling the population density of the knapweed gall-fly. Cannibalistic activities of *E. longavena* probably prevented a major change in the proportion of *E. longavena* to *P. pirata* between June 12 and June 27 (Fig. 22). As the season advanced, feeding activities of *E. longavena* continued to reduce both the *P. pirata* population (Fig. 22) and the number of galls containing *P. pirata* (Fig. 20). Once all *P. pirata* in a gall were consumed, there was an increase in the percentage of galls containing only *E. longavena* (Fig. 20, July 5). *E. longavena* perished if they did not obtain sufficient food before the supply of *P. pirata* was depleted. This was indicated by a decrease in percentage of galls containing *E. longavena* between July 5 and July 14 (Fig. 20). The first larvae of *G. stigma* appeared June 27 although this species was not abundant until later in the season. Larvae of *Habrocytus sp.* had only a slight influence on the *P. pirata* population in the first few collections in which they appeared (Fig. 22).

The occurrence of sucker shoot galls is shown by the reappearance of *P. pirata* and *E. longavena* eggs in the July 14 collection (Fig. 20). *P. pirata* were as detrimental to *D. polita* in sucker shoot galls as they were

to it in spring initiated galls. The presence of sucker shoot galls did little to increase the *D. polita* population, although they were beneficial to both *P. pirata* and *E. longavena* (Fig. 20). Only 6 galls containing a *D. polita* larva were found in the 107 sucker shoot galls collected July 23. Fall emergence of *E. longavena* enabled this species to oviposit in a large percentage of the sucker shoot galls and as a result the sucker shoot population of *P. pirata* was reduced. Because *G. stigma* larvae consumed all occupants of the galls they inhabited, their presence in 5% of the July 14 galls represented a substantial decrease in the numbers of other larvae. No *G. stigma* larvae were found in sucker shoot galls, and the inclusion of sucker shoot galls in the July 23 collection lowers the percentage of galls containing this species (Fig. 20). The presence of *E. longavena* and *P. pirata* in sucker shoot galls increased the relative abundance of these species in the July 23 collection. Had these additional larvae not been present in sucker shoot galls, the proportion of *G. stigma* and *Habrocytus sp.* would have been higher. Most of the *P. pirata* larvae in sucker shoot galls were consumed by mid-August and this also explains the further decrease in the numbers of this species (Fig. 22). Because each *Habrocytus sp.* requires one *P. pirata* larva, their presence helped decrease the number of *P. pirata* in the July 23 and August 22 collections (Figs. 20 and 22).

Fig. 23 shows the inter-relationships of all species composing the *D. polita* gall community. Although *D. polita* was the key species in the community, later in the season *P. pirata* took over the central position of the food web. *P. pirata* had the greatest influence on the *D. polita* population and the presence of this species greatly increased biomass in the community. The remaining entomophagous species depended upon *P. pirata* as their chief source of food. *Habrocytus sp.* was second

to *E. longavena* larvae as the chief predator of *P. pirata*. *G. stigma* and *T. bedeguaris* did not restrict their attack to any one species. Their importance in the community is therefore dependent upon the number of inhabitants in each gall attacked.

The most common cause of empty galls in 1968 and 1969 was food shortage. *E. longavena* and *G. stigma* larvae perished if the galls they inhabited did not contain adequate food for their development. This was less likely for *T. bedeguaris* because they oviposited later in the season when competition between entomophagous species was nearing its climax. The interior of empty galls often contained remains and particles of gall tissue. 8% of the empty galls from the two seasons contained only the remains of first instar larvae of *P. pirata* and had no internal chamber development. Abnormal environmental conditions in the gall cavity or some abnormal physiological condition of the plant tissue may have had a toxic effect which killed the gall inhabitants. In some cases *P. pirata* females may have killed the immature *D. polita* larva and then refrained from ovipositing. About 15% of the empty galls in the August 22 collection contained fungus. This fungus may have initially attacked plant tissues resulting in the death of the inhabitants or it may have developed on dead inhabitants and subsequently spread throughout the gall interior. Disease undoubtedly contributed to the fatality of some inhabitants.

Once the galls matured and fell to the ground, no further population changes took place and by analysing collections of these galls, climax of the succession was fixed. Galls are unique for studying population changes in insect communities because one can easily obtain data on succession. After analysing the percentage of galls containing each

species (Fig. 20) and the relative abundance of each species (Fig. 22), one can predict population trends for the following season. Predictions of this nature are dependent upon many factors, such as weather, which may have varying effects on the emergence of each species. It was obvious that the occurrence of *D. polita* in 9% of the 1968 mature galls was sufficient to allow for an abundance of galls in 1969. This indicates that the *D. polita* gall community is constructed to tolerate low numbers of the gall former. Several authors have found the same for other galls (Askew, 1961; Evans, 1967; and Gordinier, pers. comm.). By the end of 1969, the *D. polita* population was reduced and initial field observations in 1970 indicated that the galls were much less common than in 1969. The occurrence of *P. pirata* larvae in 27% of the 1968 mature galls was probably responsible for the decrease in the *D. polita* population by the end of 1969. The availability of *P. pirata* larvae would allow for the increase in the *E. longavena* population, which in turn would be partially responsible for the increase in empty galls. Few *Habrocytus sp.* larvae were found in 1968 mature galls and their abundance in 1969 again is probably due to the increase in the *P. pirata* population. The decrease in numbers of *G. stigma* from 1968 to 1969 is due to some unknown factor affecting only the behavior of this species. For the 1970 community population, I predict a large increase in *D. polita* larvae, this being due to a decrease in the abundance of *P. pirata*. A decrease in *P. pirata* larvae would also cause a decrease in all entomophagous species and this again reflects the importance of *P. pirata* in the gall community. This reduction of entomophagous species would allow for a 1971 increase in the *P. pirata* population and this in turn would be responsible for again decreasing the *D. polita* population.

In conclusion, it has been shown that the gall former prepared and provided requisite conditions for the inquiline, which in turn provided requisite conditions for the entomophagous species. As the season advanced, numbers of the gall formers decreased and the inquilines and entomophagous species increased. By the end of the season, the community consisted of a much larger proportion of inhabitants other than *D. polita*.

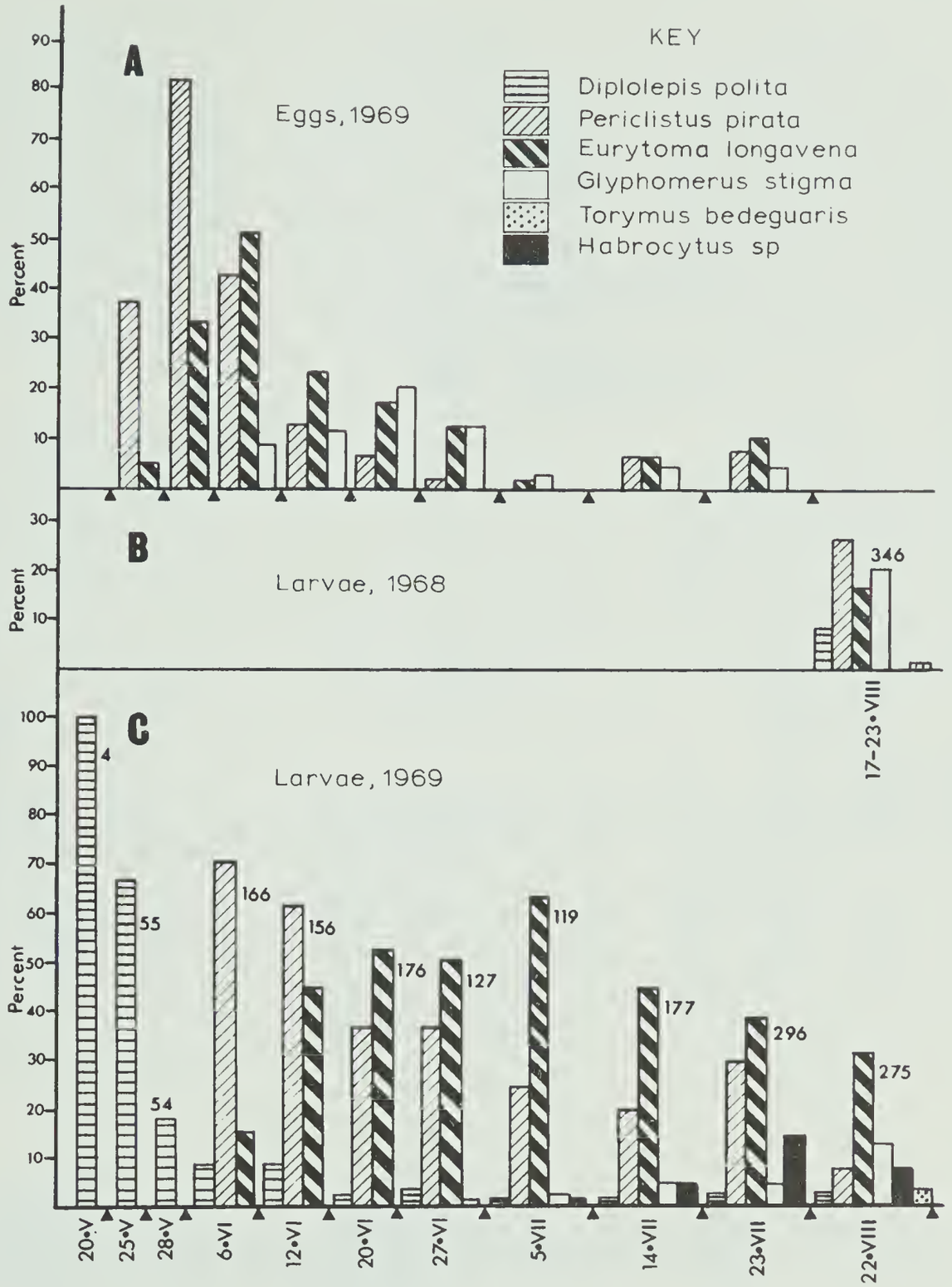


Fig. 20. Percentages of galls containing members of the Diplolepis polita gall community. Number of galls in each collection is indicated. George Lake, Alberta. 1968 and 1969. A. Eggs found in galls collected May to August, 1969. B. Larvae found in mature galls collected August 17-23, 1968. C. Larvae found in galls collected May to August, 1969.

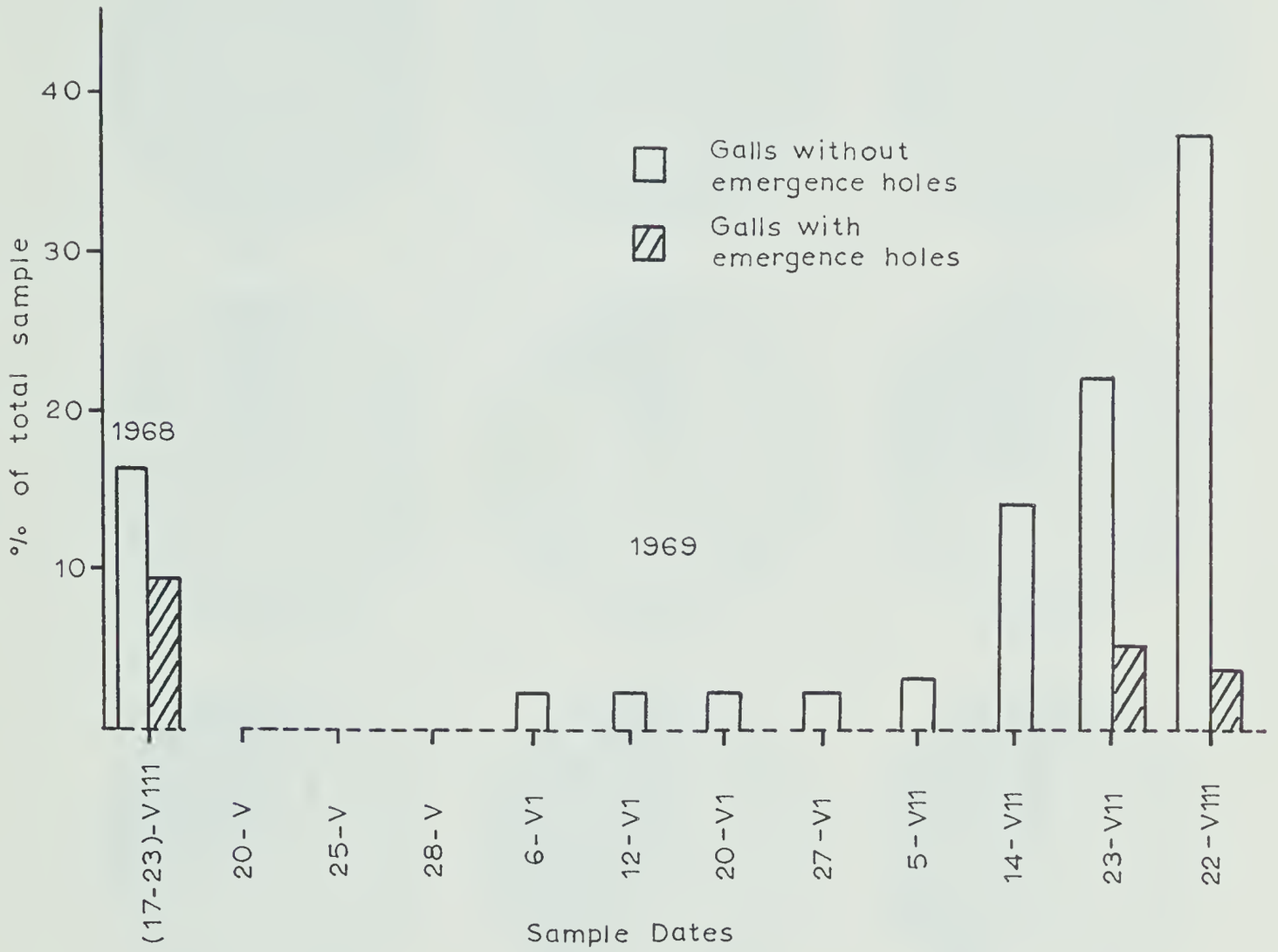


Fig. 21. Incidence of empty Diplolepis polita galls. George Lake, Alberta. 1968 and 1969.

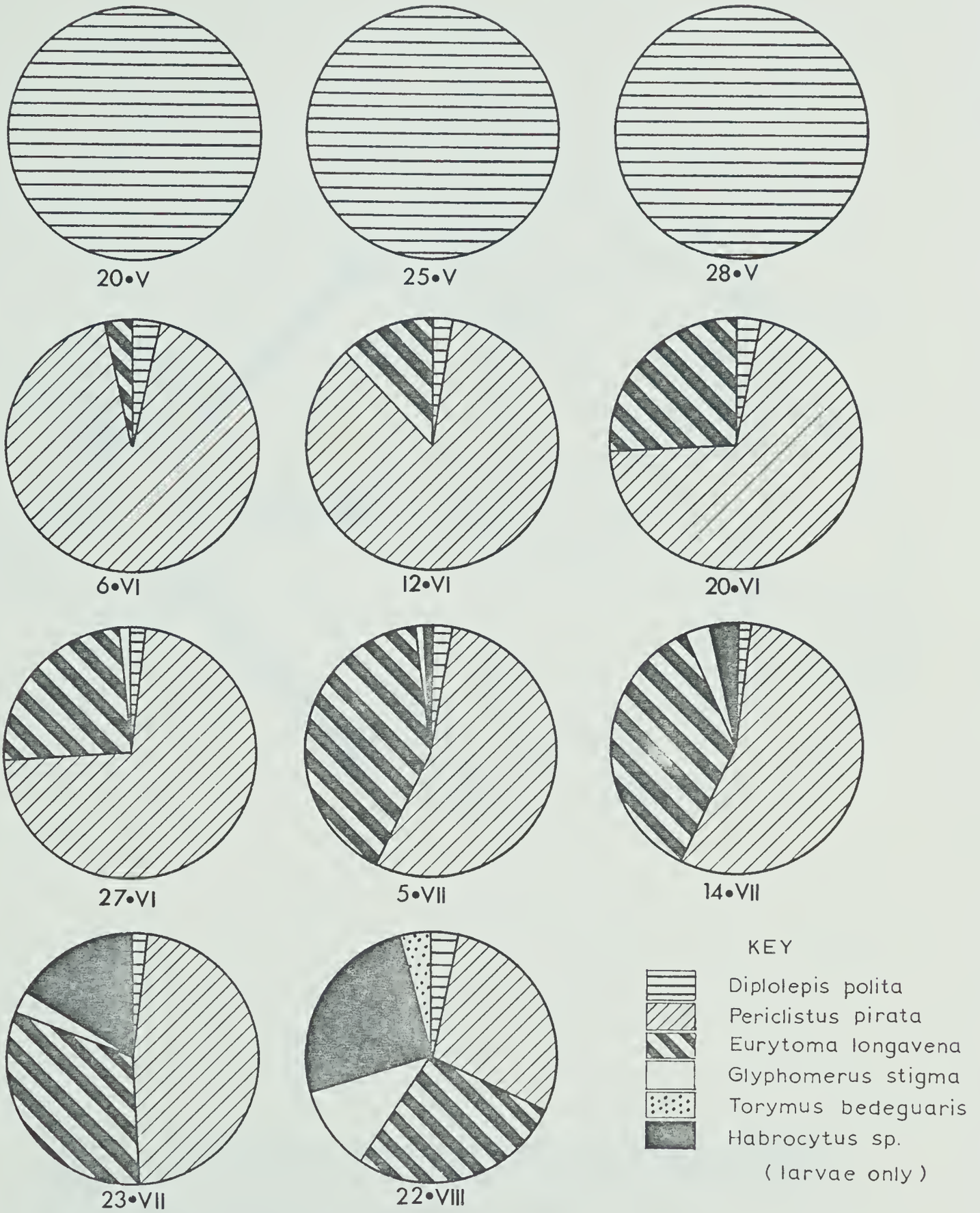


Fig. 22. Incidence of species in the Diplolepis polita gall community expressed as percentage of the total populations of gall inhabitants. George Lake, Alberta. 1969.

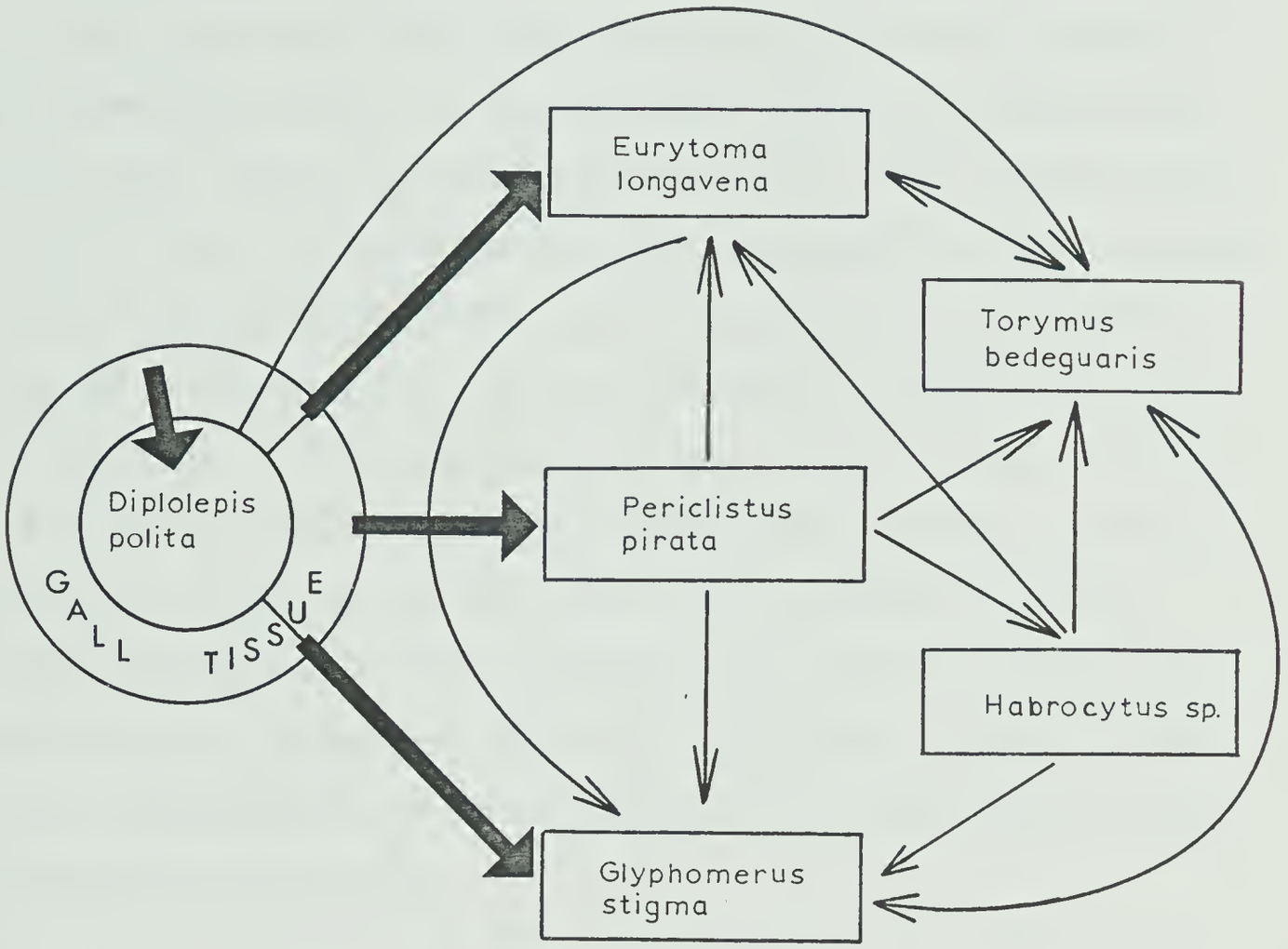


Fig. 23. Food web of species associated with the Diplolepis polita gall community. George Lake, Alberta. 1968 and 1969. Heavy line represents phytophagous habit, narrow line represents entomophagous habit.

III. Gall Growth and Developmental Morphology

A) Gall Growth Studies

a) Introduction

The objective of this section is to correlate seasonal changes in gall dimensions with gall contents. Galls inhabited by inquilines are often larger than galls containing only the gall former (Section IIIAd). In this section the growth rate of galls inhabited by a single *D. polita* larva is compared to the growth rate of galls inhabited by *P. pirata* eggs and larvae (Fig. 25). The mean diameter of 44 mature galls (Fig. 25) collected in 1968 and containing only a single *D. polita* larva was 3.8 mm. (S.D. = 0.47). McCracken and Egbert (1922) stated that the *D. polita* gall varies in size from 5 to 10 mm. in diameter and often harbours inquilines. Their measurements were probably from inquiline modified galls, rather than normal galls containing a single *D. polita* larva. The appearance of immature galls on rose sucker shoots is also discussed in this section.

b) Methods

All studies on gall growth were made in 1969 and the field search for both galls and adults began May 7, 1969. No leaves of *R. acicularis* were out at this data, although those of *Populus* and *Salix* were just appearing. The first *R. acicularis* leaves were found May 8, 1969 and these were in areas of greatest illumination. By May 11, 1969, immature leaves were present on nearly all rose plants in the study area. The first *D. polita* galls were collected May 20, 1969 and this small collection consisted of 2 leaves with 2 galls on each. From May 25, 1969 and on, galls were much more common. The diameters of all galls in the 11

random collections described previously were recorded and correlated with gall contents. The mean size of galls containing either a *D. polita* larva or *P. pirata* eggs or larvae, for all collection dates, is presented in Tables 5 and 6. In another study, 80 one square metre quadrats were randomly marked off in 4 different rose patches in the study area. A total of 134 galls on 30 leaves were found within these quadrats. Each gall was examined and measured approximately every 7 days and data were obtained on their growth rate, shrinkage, senescence, and abscission. Once the galls had fallen, they were returned to the laboratory for dissection. Sample growth curves of these galls are given in Fig. 26.

c) Growth of *Diplolepis polita* Inhabited Galls

It is well established (Section IIBc) that gall formation is due to larval feeding, and presuming that proliferation begins soon after the larva commences feeding, the period between oviposition and hatching can be estimated. Yasumatsu and Taketani (1967) estimated that the egg stage for *D. japonica* lasts from 7 to 10 days. If the length of the *D. polita* egg stage is similar to that of *D. japonica*, it can be estimated that oviposition in this species took place around May 10 in 1969 and as a result the first visible growth occurred between May 20 and May 25. But, because no adults were collected when extensive field searching began (May 7, 1969), length of the egg stage may be much longer. Adult emergence and oviposition probably take place in late April or early May.

An estimate of the growth curve for a normal gall containing a single *D. polita* larva has been included in Fig. 25. By studying growth curves of plot galls (Fig. 26), it can be estimated that the maximum size of a normal *D. polita* gall would occur around the middle of July. After this

date, there would be shrinkage and the final size due to gall maturation would be reached by the middle of August. The average amount of shrinkage or decrease in gall diameter for the 134 plot galls was .82 mm. (S.D. = 0.57) indicating that some of the mature *D. polita* galls collected August 22, 1969 (Table 5) could have been as large as 5.5 mm. in diameter at the time they were immature and still growing.

As can be seen in Fig. 25, there was a large variation in the size of galls containing a *D. polita* larva. Growth rate and condition of the host plant probably affects growth rates of attached galls. Factors such as soil condition and availability of light and water affects plant growth rates and must also influence growth rates of galls. Ovipositing in buds not in a suitable condition for galling could affect gall size. Positioning of the gall on the leaflets, the number of leaflets per leaf, and the number of galls per leaflet and leaf, could also influence gall size. Galls growing on older plants may have a different growth rate and final size compared to galls growing on younger plants and rose sucker shoots.

Although *R. acicularis* sucker shoots probably begin growing early in spring, they were first observed near the end of June in both seasons. Sucker shoots are sterile and have larger and more succulent leaves than do the older plants. Sucker shoots grow rapidly and most attained a height of 0.9 metres by the season's end. Their stems are densely spined and the tall thin plants produce few side branches. New sucker shoots were more common around open areas such as *Ledum* bogs and artificial clearings than they were in the forest. The first immature galls, all less than 2.9 mm. in diameter, were found on one of these sucker shoots July 14, 1969. As the season advanced, immature galls on these shoots

became more abundant and several collections were made up to August 13. Fig. 24 shows an increase in the number of immature galls less than 4.0 mm. in diameter on July 14. Each collection contained a decreasing number of immature galls less than 4.0 mm. in diameter as maturation processes began (Fig. 24), but the July 14 collection, and the three that followed, showed an increase in the number of immature galls. This increase illustrates the appearance of sucker shoot galls. In the July 23 collection, 106 of the 296 galls were from sucker shoots and 6 of these contained a *D. polita* larva (Table 5). Sucker shoot galls less than 4.0 mm. in diameter from 2 further collections (July 28, 1969 and August 13, 1969) are included in Fig. 24, but unfortunately contents data on these galls were not obtained. All galls in the August 22, 1969 collections were mature and the sucker shoot galls in this collection were combined with spring initiated galls (Fig. 20). Sucker shoot galls are somewhat different in appearance from spring initiated galls, for they are often more densely spined, with these spines long and hair-like. Their colour is either dark or light green, frequently with a tinge of red, in contrast to the yellowish brown of spring initiated galls.

Immature galls appearing on sucker shoots in July could be due to a delayed hatching mechanism, as mentioned by Yasumatsu and Taketani (1967). They found that *D. japonica* has two periods of gall formation, each appearance of the galls being dependent on the length of time before hatching. They reported that the first group of galls began developing 7 to 10 days after oviposition and the second type began developing 40 days after oviposition. It is possible that the increase in the number of immature *D. polita* galls near the middle of July is a result of this delay, as was found with *D. japonica*. If all *D. polita* eggs were laid

Table 5

Mean diameters of galls containing one larva of *Diplolepis polita*. George Lake, Alberta. 1969.

Date	No. of galls in collection	No. of galls containing *D. polita*	Mean size of galls containing *D. polita* larva (S.D.)	
20-V	4	4	0.8	(0.05)
25-V	55	35	0.9	(0.4)
28-V	54	10	1.9	(0.6)
6-VI	166	15	2.4	(1.0)
12-VI	156	13	3.2	(1.3)
20-VI	176	9	3.3	(1.2)
27-VI	127	4	3.7	(1.1)
5-VII	119	4	3.4	(0.7)
14-VII (spring)	156	2	-	-
14-VII (sucker)	21	-	-	-
23-VII (spring)	190	2	-	-
23-VII (sucker)	106	6	1.7	(0.3)
22-VIII	275	7	4.3	(0.6)

spring = galls initiated in the spring only

sucker = galls initiated on sucker shoots only

around May 1, this second group of immature galls could be developing after approximately 70 days' hatching delay. Although all 13 immature galls collected July 14 contained *P. pirata* eggs, the remains of a *D. polita* larva were found in 5 of them, indicating these galls were caused by *D. polita*. The presence of 6 *D. polita* galls in the July 23 collection of 106 immature galls adds weight to this hypothesis. It is proposed that hatching of the eggs laid in buds of sucker shoots is delayed for a greater length of time than is the hatching of eggs laid in buds of older plants. This delay could be due to some physiological or biochemical condition within the host plant. Once the delay mechanism is no longer present, there is an increase in the number of immature galls later in the season.

d) Growth of *D. polita* Galls Inhabited by *P. pirata*

As discussed in Section IIBc, *P. pirata* cannot be considered a true inquiline. Larvae of *P. pirata* can cause the proliferation of meristematic type cells already present in the immature *D. polita* galls. In Section IIIBe, it is shown that internal chamber formation by *P. pirata* larvae causes structural and developmental changes in the host gall. Besides introducing structural modifications, the combined feeding activities of the larvae also cause gall size to increase. Although many authors have discussed the position of 'inquilines' in gall communities, few have mentioned their ability to increase gall size. Niblett (1947) was one of the few to show this and stated that the *Diplolepis* gall he was studying showed a great variation in size when inhabited by *Periclistus* larvae. Blair (1945) maintained the opposite for the inquiline *Synergus reinhardi* Mayr found in the galls of *Cynips kollari* Hartig, suggesting that inquiline

larvae may inhibit gall growth. Evans (1967) stated that if the *Besbicus mirabilis* (Kinsey) gall is inhabited by the inquiline *Ceroptres* species, the immature gall ceases to grow and becomes hard and brittle. Yasumatsu and Taketani (1967) found that galls of *D. japonica* attacked by *Periclistus sp.* were irregular in shape, but they made no mention of size changes.

18 of the 55 *D. polita* galls collected May 25, 1969, contained eggs of *P. pirata* and in all 18 the larva of *D. polita* had been killed. In the May 28 collection, 44 of 54 galls contained *P. pirata* eggs and the mean size of the 44 galls was larger than the mean size of the 10 galls containing a single *D. polita* larva (Fig. 25). As discussed in Section IIIBe, feeding of the *P. pirata* larvae on the gall's interior results in each larva becoming encased in an inner chamber. Initiation of inner chamber development was first observed June 20, 1969 and by July 14, chambers were completed in 82% of the galls containing *P. pirata* larvae. The largest spring initiated gall containing *P. pirata* larvae was found July 5, 1969 and it was 12.4 mm. in diameter.

The increased size of galls containing *P. pirata* eggs (Table 6) indicates that the presence of eggs of this species causes additional cell proliferation. Chemicals that cause the proliferation could be injected into gall tissue at the time of oviposition or the eggs may secrete activating chemicals. Once hatched, larval feeding activities also contribute to the increase in gall size and this size may also be influenced by the number of either eggs or larvae present. The presence of *P. pirata* eggs in 72% of the 166 galls collected June 6, 1969 showed that a large percentage of the galls formed by *D. polita* are influenced by this 'inquiline' species. Fig. 20 shows that the number of galls

containing *P. pirata* larvae decreases as the season progresses. Larvae of *E. longavena, G. stigma, T. bedeguaris,* and *Habrocytus sp.* attack *P. pirata* larvae and in most cases destroy all larvae present (Section IIBc). Even though a predator may destroy all gall inhabitants, gall size in most cases would have been previously influenced by *P. pirata* larvae (Growth curves C, D, and E, Fig. 26). Although both galls contained predators when dissected, cell and chamber remains indicated that the galls once contained *P. pirata* larvae. Predation after *P. pirata* had influenced gall size, resulted in many large galls without *P. pirata* chambers. This was also recorded by Niblett (1947). I collected numerous galls in the latter part of both seasons that were over 7.0 mm. in diameter, not containing predators, but having only one or two *P. pirata* chambers. Niblett (1947) also noted the peculiarity of smaller galls containing several inquilines and some larger galls containing only one or two inquilines. Growth curves A and B (Fig. 26) show that the number of *P. pirata* chambers in mature galls is not an indication of the effect *P. pirata* has had on the gall. Mature galls larger than 5.0 mm. in diameter and containing one *P. pirata* chamber, have probably been influenced by several *P. pirata* larvae earlier in the season. A gall containing *P. pirata* and attacked by a predator early in the season, would probably not attain as large a size as would a gall with *P. pirata* larvae attacked after some chamber formation had occurred. In this attempt to show that abnormal gall size is due to feeding activities of *P. pirata,* only the galls containing *P. pirata* larvae are shown in Fig. 25.

Galls formed on sucker shoots later in the season are also attacked by *P. pirata.* Another characteristic of sucker shoot galls is that they do not attain the size of *P. pirata* enlarged galls that were initiated in

Table 6

Mean diameters of *Diplolepis polita* galls containing eggs or larvae of *Periclistus pirata*. George Lake, Alberta. 1969.

Date	No. of galls in collection	No. of galls containing eggs or larvae	Mean size of galls containing eggs or larvae (S.D.)
20-V	4	0	- -
25-V	55	18 (eggs)	1.6 (0.7)
28-V	54	44 (eggs)	3.5 (0.8)
6-VI	166	119 (larvae)	5.0 (1.4)
12-VI	156	96 "	6.4 (1.5)
20-VI	176	64 "	6.4 (1.7)
27-VI	127	45 "	6.5 (1.6)
5-VII	119	29 "	7.0 (2.0)
14-VII (spring)	156	35 "	6.9 (1.9)
14-VII (sucker)	21	17 (eggs & larvae)	3.2 (1.3)
23-VII (spring)	190	33 (larvae)	8.1 (1.6)
23-VII (sucker)	106	53 "	4.6 (1.0)
22-VIII	275	21 "	7.2 (1.9)

spring = galls initiated in the spring only

sucker = galls initiated on sucker shoots only

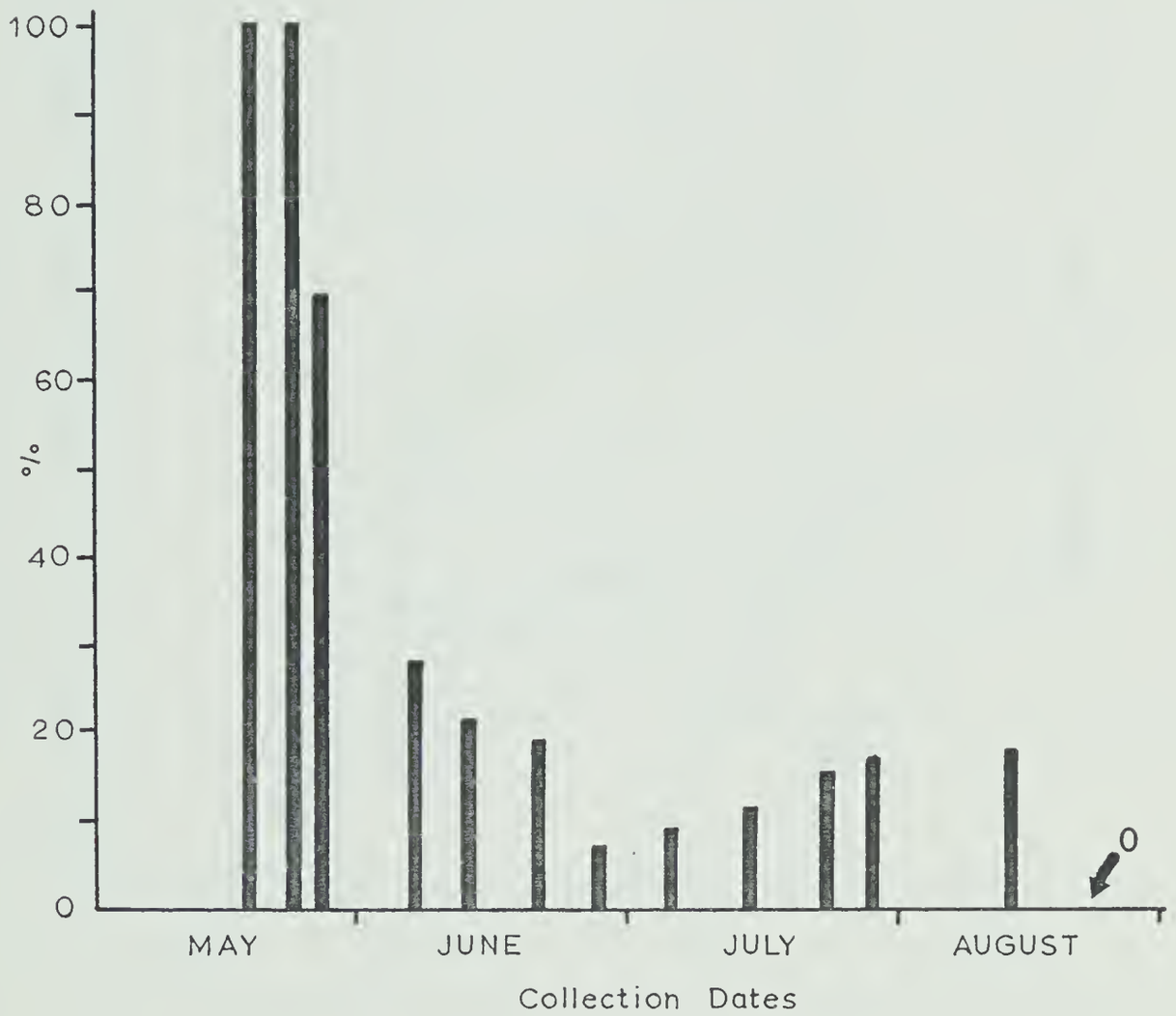


Fig. 24. Seasonal change in the numbers of immature Diplolepis polita galls less than 4.0 mm. in diameter, expressed as a percentage of each gall collection. George Lake, Alberta. 1969.

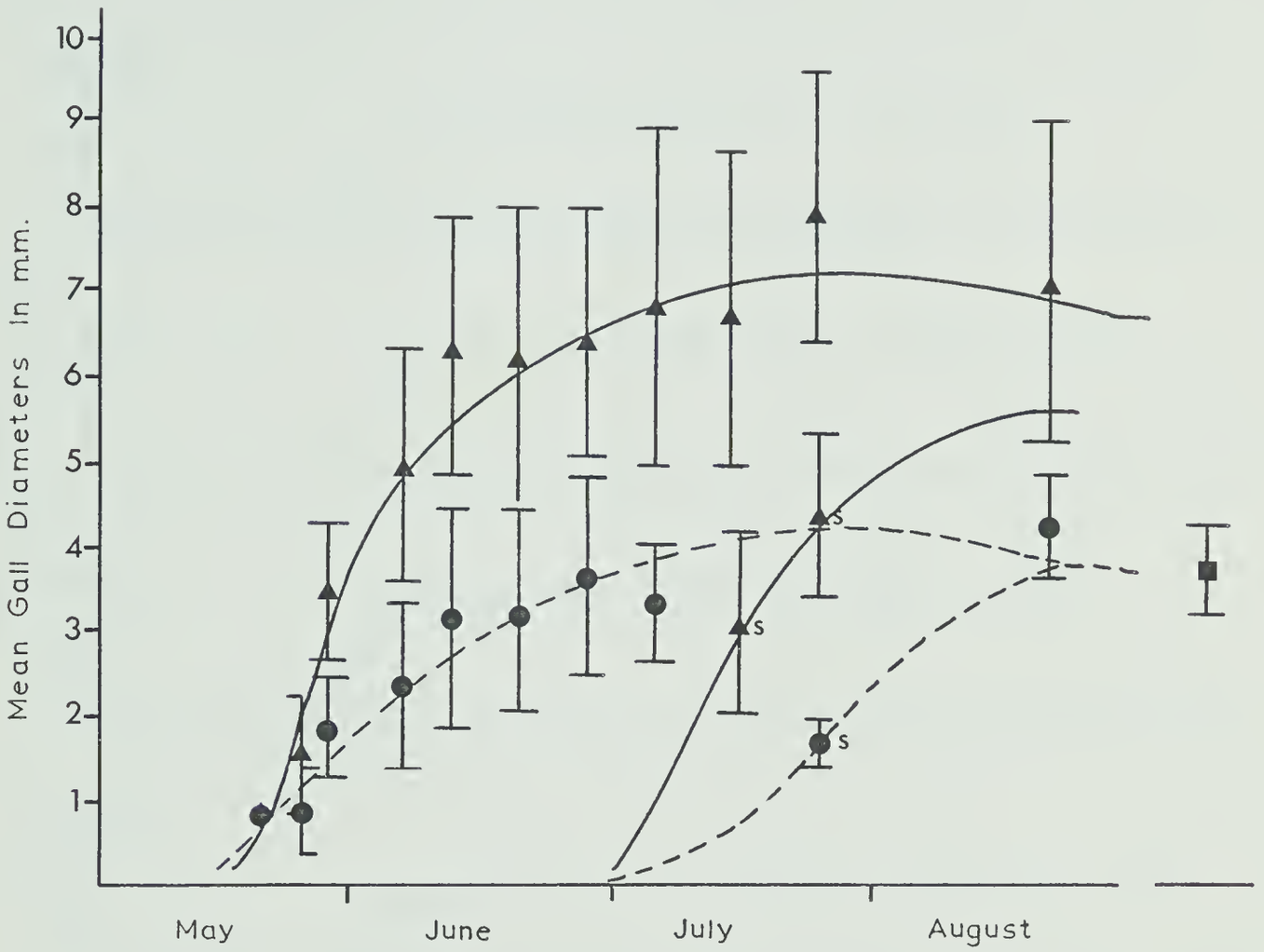


Fig. 25. Seasonal change in the mean size of galls containing a single Diplolepis polita larva compared to galls containing Periclistus pirata eggs or larvae only. Diplolepis polita ● ; 1968 Diplolepis polita inhabited galls ■ ; Periclistus pirata ▲ ; Sucker shoot galls s . Vertical lines indicate one standard deviation each side of the mean. George Lake, Alberta. 1968 and 1969.

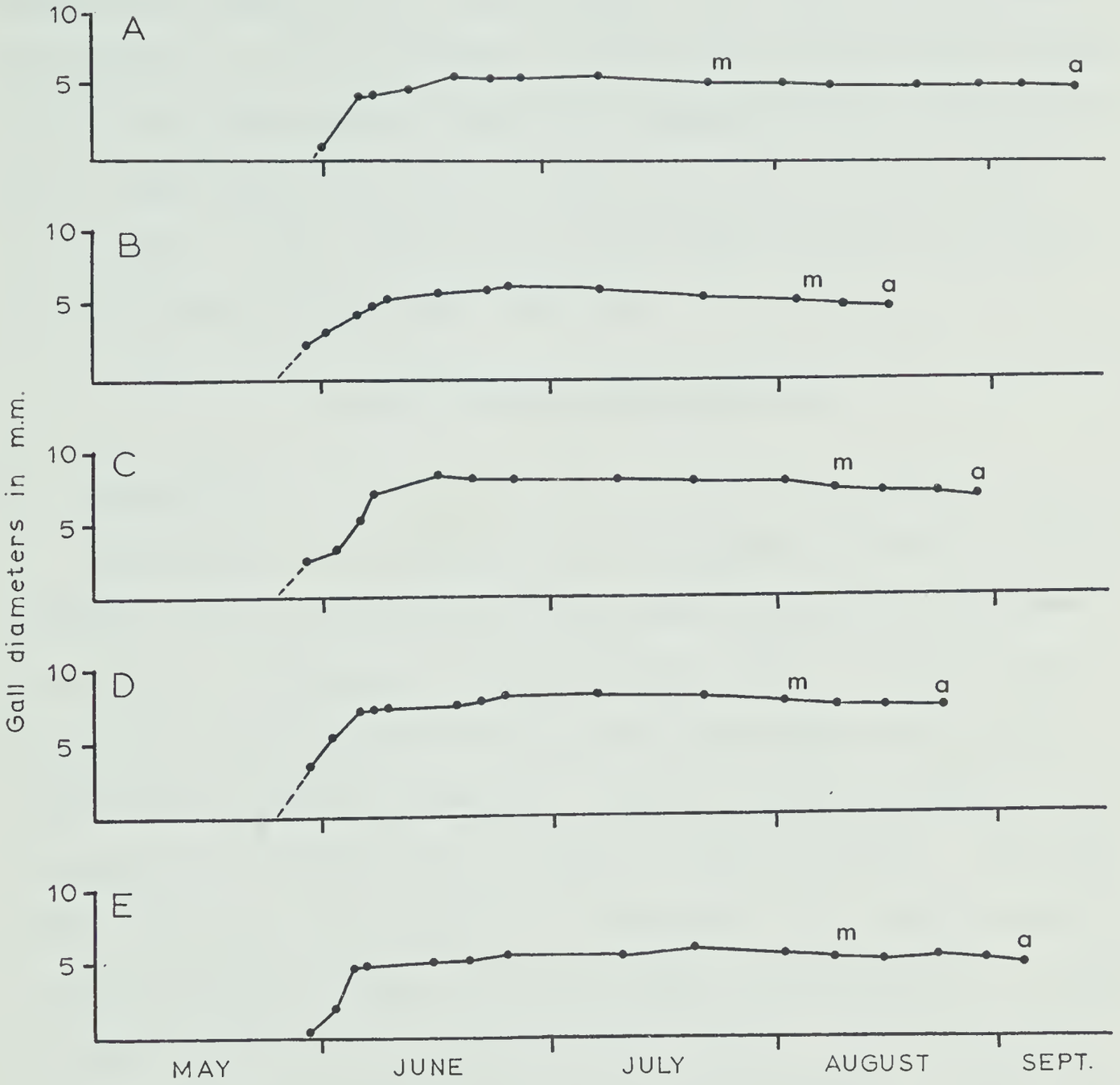


Fig. 26. Growth curves of Diplolepis polita galls inhabited by various members of the gall community. (m) approximate date of maturation; (a) approximate date of abscission. A. Gall containing 6 Periclistus pirata chambers. B. Gall containing 1 Periclistus pirata chamber. C. Gall containing 1 Periclistus pirata chamber, 1 Eurytoma longavena larva and cell fragments. D. Gall containing 1 Eurytoma longavena larva and all Periclistus pirata chambers destroyed. E. Gall containing 1 Glyphomerus stigma larva and no Periclistus pirata chambers.

the spring. Physiological conditions of the host plant allowing gall formation may change as the season advances. The largest sucker shoot gall found was 6.4 mm. in diameter. Of the 106 sucker shoot galls found July 23, 1969, 50% contained larvae of *P. pirata* and 94% of these galls had no inner chamber development. Mean size of these 53 galls was 4.6 mm. (S.D. = 1.0), significantly smaller than the mean of 8.1 (S.D. = 1.6) for spring initiated galls (Fig. 25).

B) Gall Developmental Morphology

a) Introduction

Cecidogenesis, the biology of gall developmental morphology, embraces a complex series of interactions between plant tissues and gall former. Correlation of histological and developmental studies of the gall with activities of the inhabitants aids in the understanding of the interrelationships of the gall community. Because of these interactions, gall development and growth can be considered ecological problems. The fundamental difference between growth and development is now widely recognized. I consider growth a change in size and weight, and development, a sequence of internal changes with a rearrangement of tissues. The rate of gall development does not depend upon the rate of gall growth. A small slow-growing gall can still exhibit normal development.

The cells composing insect galls are nearly always larger than normal host cells (Fig. 33). Mani (1964) stated that there is an increase in the water content and an increase in the number of vacuoles in gall cells. In the *D. polita* gall, abnormal thick-walled and thin-walled cells are formed from mesophyll cells. The appearance of cell abnormalities such as retarded separation of chromosomes, binuclear and

nuclear hypertrophy are common phenomena of gall cells (Mani, 1964). Hough (1953) suggested that gall cells are biochemically different from normal cells. In reference to the widely accepted concept that some plant tissues are capable of developing into other kinds of tissue, it is not surprising that hairs and spines can develop from gall tissues.

As in nearly all cynipid galls, the *D. polita* gall is a structure of determinate growth and uniform size. It has a form which differs from anything normally produced by the host. Gall tissues are organized in very different and definite tissue patterns.

It is the objective of this section to show how *D. polita* and *P. pirata* influence the *R. acicularis* tissue in the process of gall formation.

b) Materials and Methods

D. polita galls and leaf tissues of *R. acicularis* were collected throughout the seasons of 1968 and 1969 and all tissues were fixed in F.A.A. solution. Immature galls 4 mm. or less in diameter were fixed whole, but larger galls were halved or quartered to allow adequate penetration of the fixative. Dissection was also necessary to determine gall contents. All tissues were stored in the fixative until required for sectioning. In preparation for sectioning, the tissues were dehydrated in n-butyl alcohol. Following dehydration, infiltration was accomplished by placing the tissues in a n-butyl alcohol and tissuemat mixture and then into pure tissuemat. Considerable difficulty was experienced in embedding larger galls without the formation of air bubbles in the wax. A technique was developed whereby the blocks were cooled slowly by gentle blowing of the breath, rather than plunging them

into cold water as is usually recommended. The embedded tissues were sectioned at 10 microns on a rotary microtome. Mature galls were found to be hard and brittle and difficult to section. Blocks containing mature galls were cut until tissue was exposed on the cutting face and then immersed in a solution of half 50% alcohol and half glycerol. It was often necessary to leave the blocks in the media for two weeks. All sections were stained by a combination of 1% aqueous safranin and 0.2% fast green in 95% alcohol.

c) Gall Induction

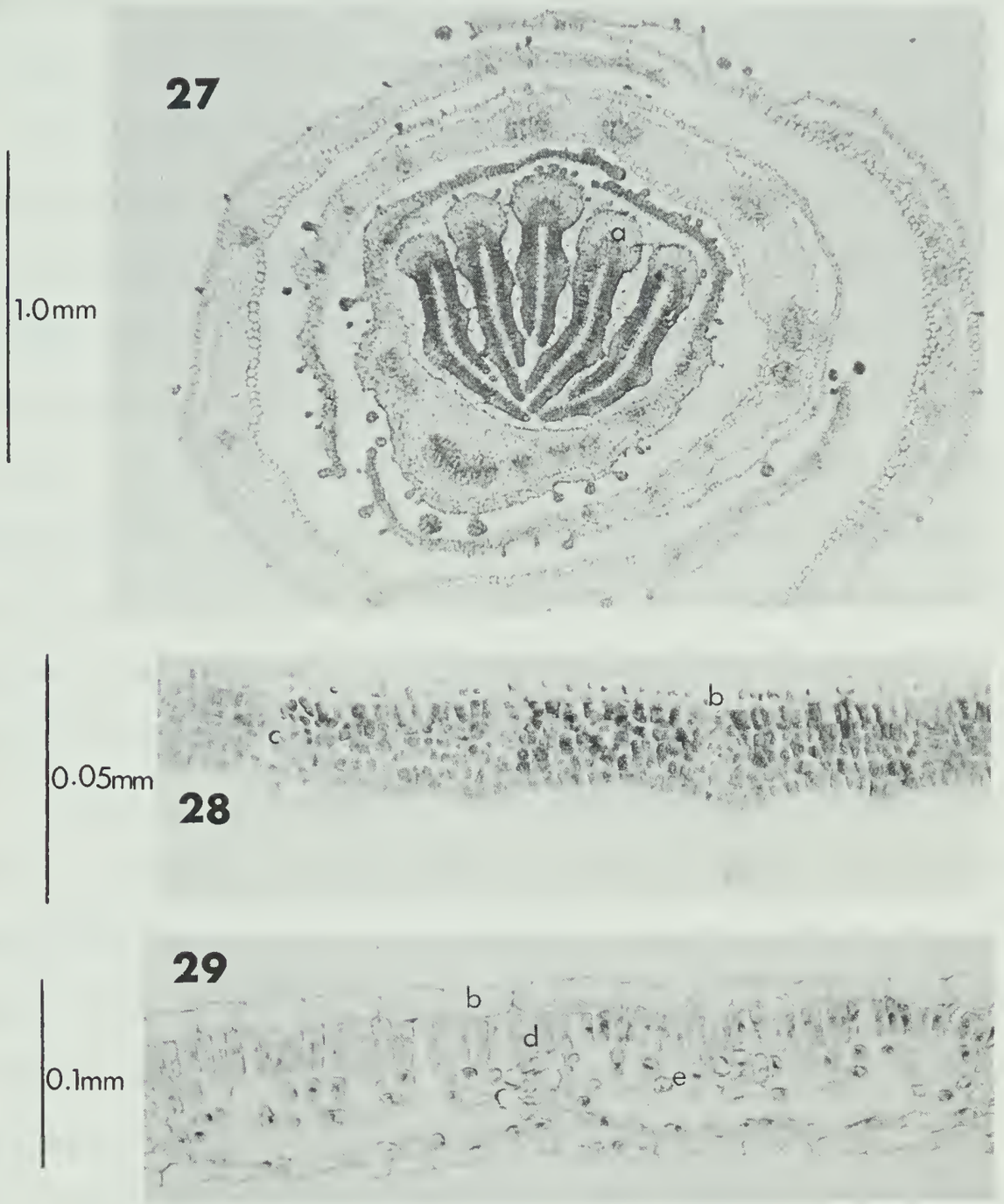
The initial stimulus for cynipid gall formation is now considered by most workers to be chemical in nature. Plumb (1953) and Mani (1964) have reviewed the literature concerning theories of gall initiation. Adler (1894) was the first to observe that cynipid galls did not begin development until the larva had hatched. Cook (1903) contended that gall formation was the result of mechanical stimulation of the plant cells by the larvae. Kostoff and Kendall (1929) believed that the presence of bacteria in the vicinity of the developing larva was responsible for gall formation. Triggerson (1914) suggested that the chemical stimulus came from the Malpighian tubules, but most authors are now convinced that the chemical is located in the salivary glands. It has been suggested that compounds similar to plant auxins, enzymes, or enzyme inhibitors, secreted by gall forming larvae, may be responsible for gall formation. Hough (1953) reported that experiments using macerated cynipid larvae injected into plant tissues failed to produce gall growth, but added that this cannot be considered proof that tissue stimulating substances are not present in the larvae. Hough also

suggested that something besides a simple chemical stimulus is required to produce the characteristic forms of cynipid galls. He added that the chemical stimulus must be emitted continuously with the possibility that two stimuli are required—one to initiate gall formation and the other to produce differentiation in gall tissues.

d) Development of the *D. polita* gall

To explain changes occurring in gall development, normal immature and mature leaf tissue must be examined. Because cynipid gall formation must start when host tissue is meristematic, it can be presumed that *D. polita* oviposits in buds of *R. acicularis*. Leaf primordia are curled inside the bud and are composed of homogeneous mesophyll and epidermal cells. Fig. 27 is of a transverse section of a *R. acicularis* bud collected May 9, 1969, the approximate date of *D. polita* oviposition. Cells of the leaf primordia are in a state of rapid development and Fig. 28 shows the anatomy of a primordium in greater detail. The homogeneous mesophyll cells of the leaf primordia have not differentiated into palisade and spongy parenchyma. All cells are about the same size, are packed closely, and have dense cytoplasm. Some vascular tissue has developed and the upper epidermal cells have differentiated. Nuclei are very large compared to the cell's size and cell vacuoles are inconspicuous. In 1969, the first *R. acicularis* leaves were found May 8. Leaves newly emerged from buds have well-formed palisade and spongy parenchyma cells (Fig. 29). Because the cells have increased in size, their nuclei do not appear as large as those in homogeneous cells (Fig. 28). Conspicuous vacuoles are now present in the leaf parenchyma cells.

The starting point for the series of developmental changes involved



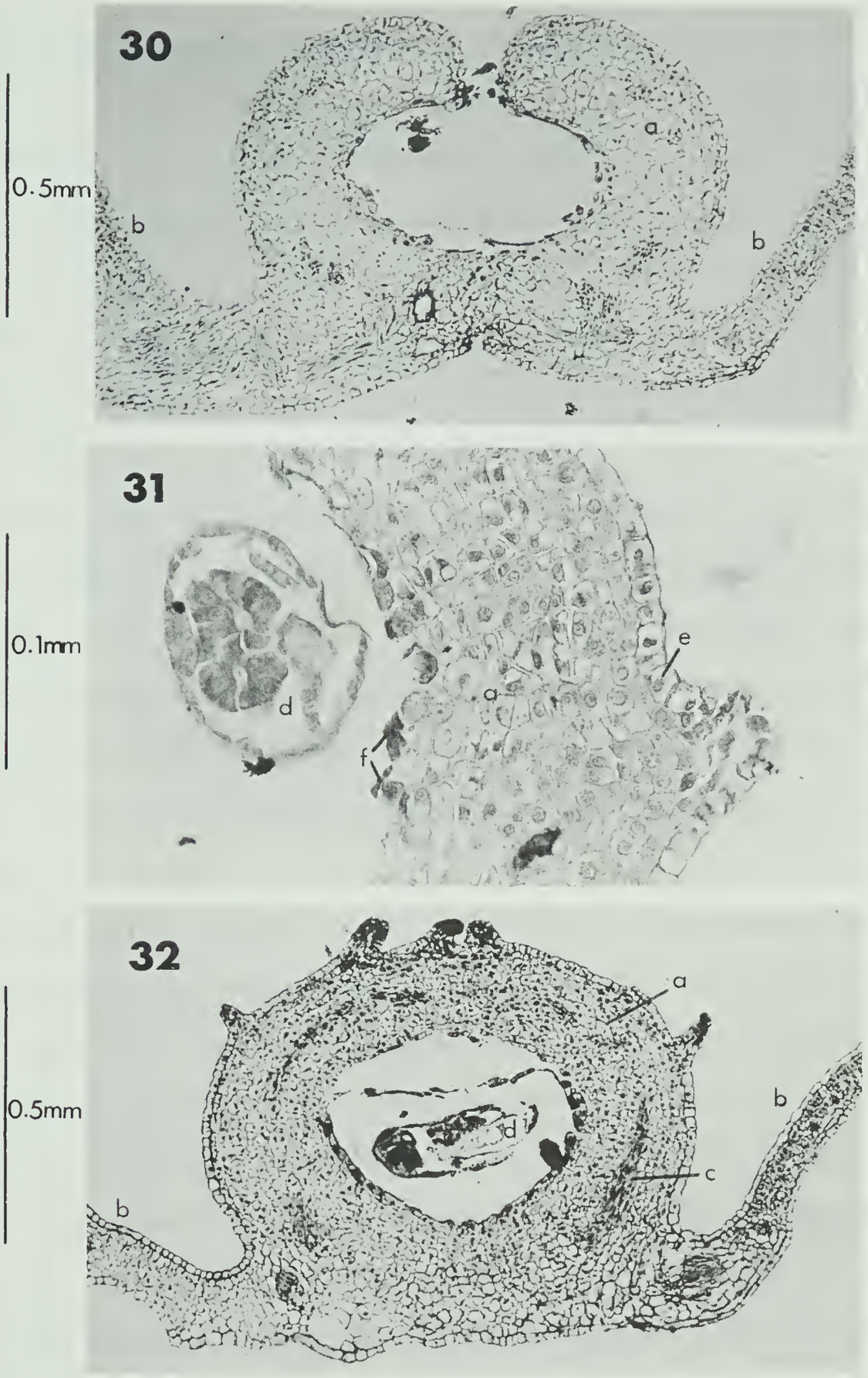
Figs. 27-29. Developmental morphology of Rosa acicularis leaves. 27. Cross section of Rosa acicularis bud, collected May 9, 1969. 28. Long. section of Rosa acicularis leaf primordium, collected May 9, 1969. 29. Long. section of Rosa acicularis leaf, collected May 28, 1969. (a) leaf primordium; (b) epidermis; (c) homogeneous mesophyll cells; (d) palisade cells; (e) mesophyll cells.

in gall formation is oviposition by the gall former. Although I have never observed *D. polita* ovipositing, Yasumatsu and Taketani (1967) showed that *D. japonica*, a leaf gall former, oviposited in buds of the host. It is not known whether *D. polita* eggs are laid on the surface of leaf primordia or inside the tissue. Beyerinck (1883) and Weidel (1911) stated that cynipid eggs can be deposited on the epidermis. Hough (1953) found that eggs of *Neuroterus quercus-baccarum* (L.) (Family Cynipidae), which forms galls on oak leaves, were laid inside host tissue. He found that some hypertrophy occurs before hatching, but suggested that this occurred when any foreign body is present. Most workers of cynipid biology have agreed that initial stages of gall development come after the larva punctures the first plant cell. Kostoff and Kendall (1929) stated that the stimulus for cell proliferation is initially applied in one area, decreasing in intensity as it spreads centrifugally. Hypertrophy (overgrowth without cell division) and hyperplasy (rapid cell proliferation) occur most intensively near the gall former. Continual gall development depends upon the feeding activities of the gall former. Many authors have shown that cynipid gall formation ceases if the larva is killed or removed.

D. polita galls begin development either when the leaf tissue is in a homogeneous condition (Fig. 28) or when leaf tissue has started to differentiate. Either way, gall formation must be initiated when leaf tissue is immature and in a plastic condition. If the newly hatched larva of *D. polita* initially feeds on the outside or near the surface of the upper epidermis of the leaf primordia, then gall tissues grow upwards and surround the larva. Weidel (1911) stated that cell proliferation starts when the presence of the larva causes degeneration of the

underlying epidermal cells. Many workers have shown that the direction of gall growth is away from the insect. Fig. 30 shows a section of an immature gall collected May 28, 1969. The gall resembles a small crater suggesting that tissues arise from around the larva and thus encase it. Tissue fusion occurs when the sides meet. In mature galls, this fusion is marked by a protrusion of tissue into the gall cavity. Cells of immature galls (Fig. 32) are homogeneous and only the epidermis is continuous with the normal leaf. Cells of the galled leaf have differentiated into palisade parenchyma and spongy parenchyma. Spines are not found on galls in the early stages of development. In several galls (Wells, 1920), cell wall formation does not follow nuclear division and multinucleate cells result. I have observed mitotic figures in *D. polita* galls and it appears that cell wall formation accompanies nuclear division.

The *D. polita* larva either prevents the homogeneous tissues of the leaf primordia from differentiating, or if the gall formation began after leaf tissues had differentiated, the presence of the larva causes the leaf tissue to dedifferentiate. Wells (1921) stated that the gall former can cause the dedifferentiation of plant tissue that would normally express host plant characters. He suggested that once the tissue had differentiated, the gall former influenced the tissue such that specific gall characters appear. He further suggested that all prosoplasmic galls begin in partially differentiated tissue involving a process of dedifferentiation. Malyshev (1968) suggested that cynipids make use of the fundamental property of plants of being able to convert definitive tissues back into meristematic tissue. Cook (1923), Kuster (1930), and Wells (1920) agreed that most galls are similar in their early stages and are



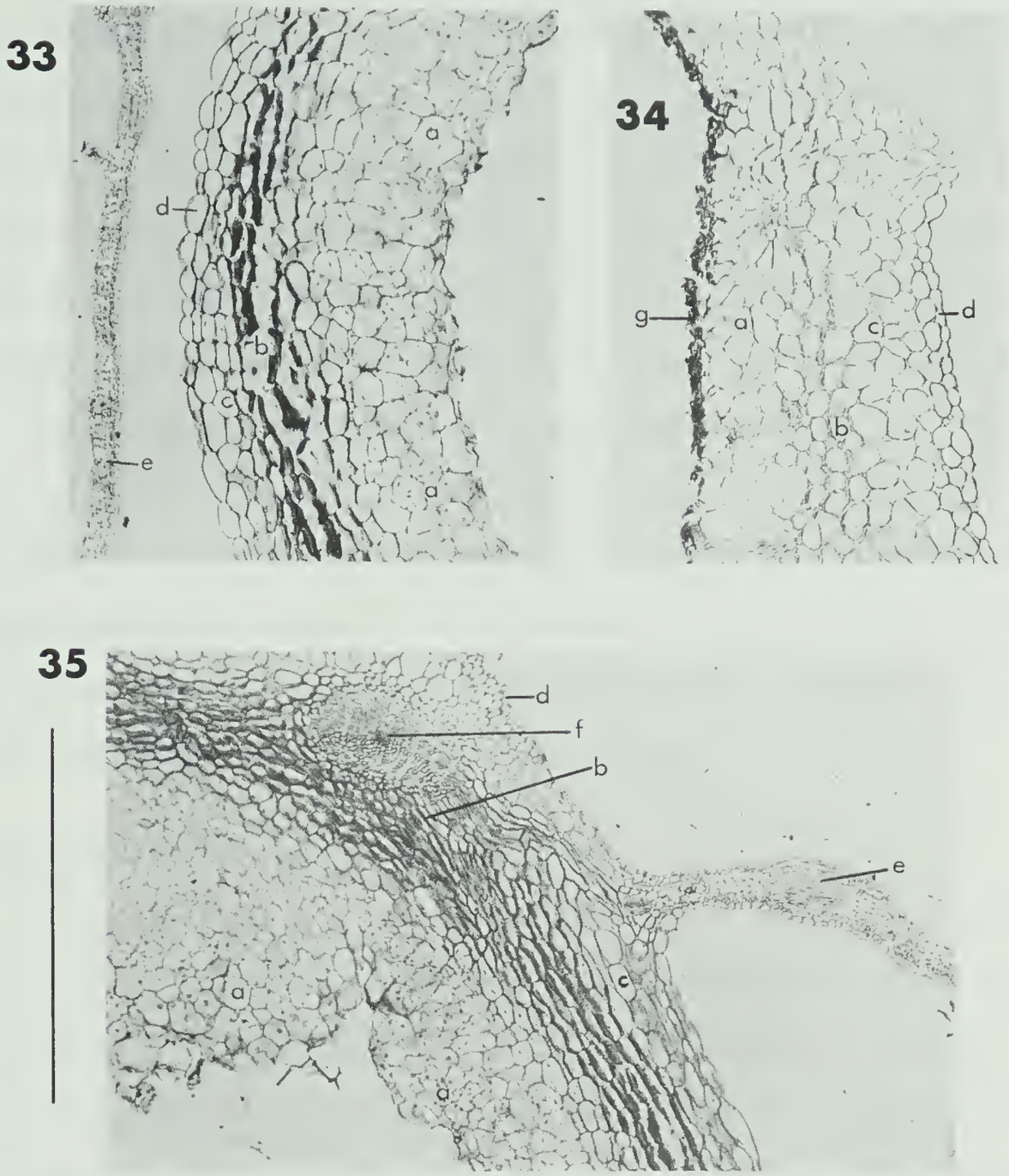
Figs. 30-32. Sections of immature Diplolepis polita galls. 30. Process of encasing Diplolepis polita larva in gall cavity. Collected May 28, 1969. 31. Section of immature gall showing cell arrangement and cells damaged by Diplolepis polita larva. Collected May 28, 1969. 32. Diplolepis polita larva encased in gall cavity. Gall tissues in early stages of differentiation. Collected June 6, 1969. (a) homogeneous cells; (b) host leaf; (c) developing vascular tissue; (d) Diplolepis polita larva; (e) epidermis; (f) cells damaged by Diplolepis polita feeding.

made up of undifferentiated tissues similar to kataplasmic galls. Once the larva is enclosed by the upward growing tissues, it finds itself surrounded by layers of young parenchyma cells (Fig. 32). Larvae of *D. polita* were observed ingesting cell contents and Fig. 31 shows collapsed cells in an area of larval feeding. At this stage gall tissue is mainly composed of homogeneous cells, although some vascular tissue is present. Epidermal cells are still plainly visible and are slightly larger than normal epidermal cells. Cells of the immature gall are characterized by their dense cytoplasm and hypertrophied nuclei and nucleoli (Fig. 31). This tissue is similar to that of leaf primordia (Fig. 28) except that the cells are arranged in a less orderly manner. Growth of the parenchyma cells does not seem to stretch or rupture the epidermal cells, although this has been recorded in other galls. Once fusion of the upward growing tissues has occurred, gall spines begin to develop.

As the larva continues to feed, further gall developments occur and the homogeneous tissues undergo diffentiation. According to Cosens (1912), the larval secretions control plant growth and development. Cells composing the tissues nearest the larva have been collectively termed the nutritive zone and even though these cells do not differentiate, they undergo extensive hypertrophy (Fig. 33). Kostoff and Kendall (1929) stated that these cells are rich in starch and proteins and are enlarged due to the abundant storage of nutritive substances. Development of the collenchyma zone takes place in the tissues beyond the nutritive zone and is clearly visible in galls collected June 20, 1969 (Fig. 33). Note the extent of the hypertrophy by comparing the size of gall cells with cells of normal tissue below the section. Beyond the nutritive zone

there develops a layer of thick-walled cells which have been described as the protective zone. Cells of this zone have been derived from the homogeneous parenchyma cells of the immature gall. In the *D. polita* gall, the zone can be as many as 6 layers of cells thick (Fig. 35). Many workers have accepted the theory that this layer of cells serves to protect the gall former within, but other authors (Cosens, 1912) suggested that any protective value was unlikely. 98% of the *D. polita* galls were attacked by predators, inquilines, or ectoparasites in 1969 indicating that the layer can hardly be regarded as advantageous to the gall former. In many descriptions of galls it is reported that this zone is composed of sclerenchyma cells. Results of phloroglucinol-HCl tests on *D. polita* galls suggest that the thick-walled cells are collenchyma rather than sclerenchyma. This zone was present in *D. polita* galls collected as early as June 6, 1969. Hough (1953) stated that the definitive sclerenchyma cells of *N. quercus-baccarum* galls arise about 14 days after the larva hatches. The presence of sclerenchyma or collenchyma cells is responsible for the rigidity of prosoplasmic galls as compared to kataplasmic galls which shrivel and shrink as the gall matures. One would expect this zone to be present in all galls similar to that of *D. polita*, but Cosens (1912) reported that the zone was absent in galls of *D. bicolor* and *D. nebulosus*. He also reported the rare feature of two separated layers of sclerenchyma cells in the gall of *D. ignotus*. Stewart (1914) found that the galls of *Andricus punctatus* Bassett (Cynipidae) contained stone cells, a cell type that does not occur in normal tissues of the host.

Beyond the layer of collenchyma cells is a second layer of parenchyma cells (Figs. 33 and 35). Because *D. polita* larvae do not feed

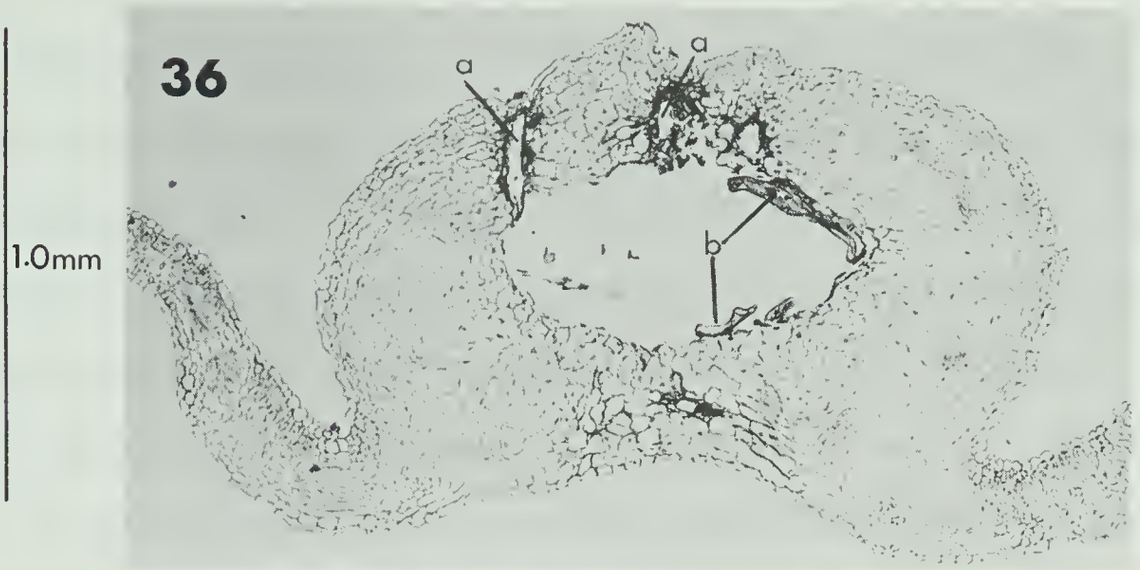


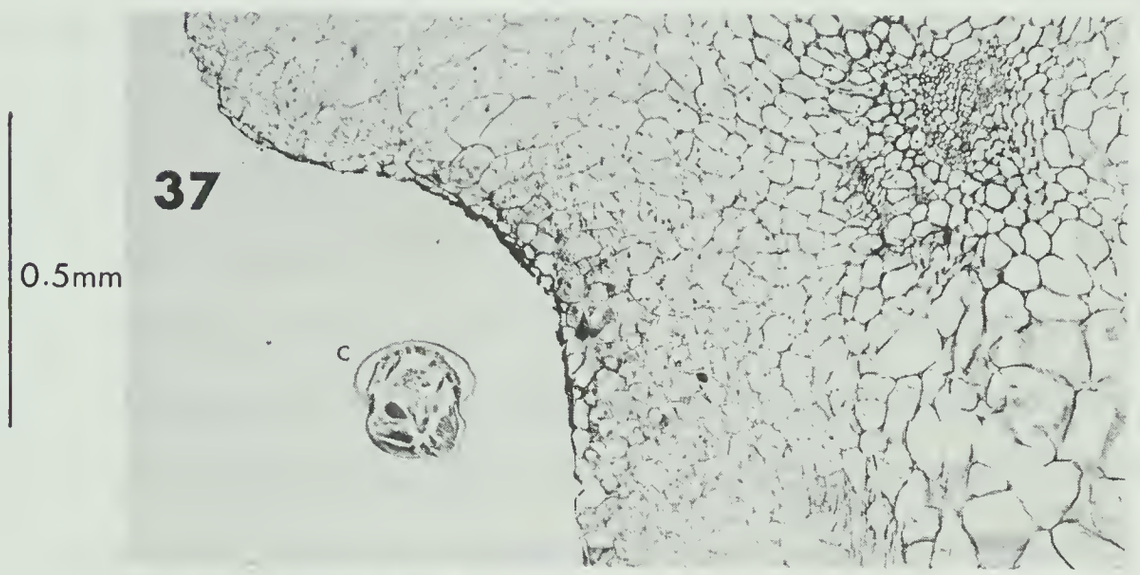
Figs. 33-35. Sections of maturing Diplolepis polita galls. 33. Section of gall wall showing differentiation into 4 zones. Note size of gall cells compared to host leaf cells to the left. Collected June 20, 1969. 34. Feeding damage of Glyphomerus stigma larva. Collected July 30, 1968. 35. Mature gall showing completion of differentiation. Collected July 20, 1968. (a) nutritive parenchyma cells; (b) collenchyma cells; (c) second layer of parenchyma cells; (d) epidermis; (e) host leaf; (f) vascular tissue; (g) cell fragments. Accompanying scale equals 1.0 mm.

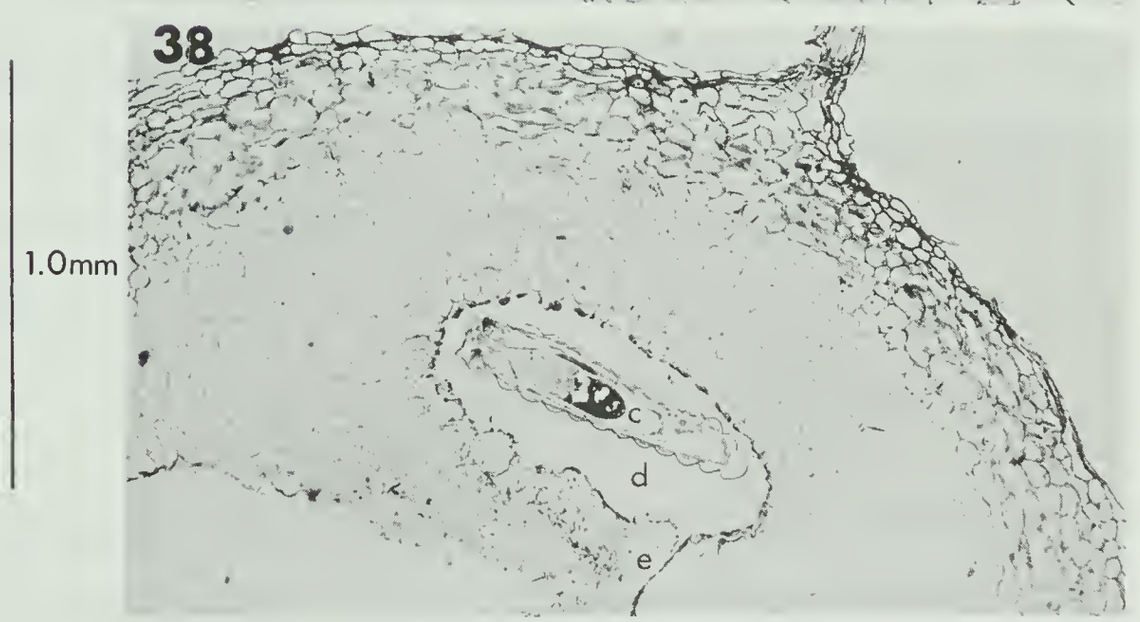
beyond the collenchyma cells, this layer of prosoplasmic cells apparently serves no direct nutritive function. The fourth layer of cells in the *D. polita* gall is the epidermis. Some of the epidermal cells in maturing galls are stretched longitudinally (Figs. 33 and 35). In many gall sections examined, the epidermal layer was poorly differentiated and was similar to parenchyma cells beneath. No stomata were observed in any of the maturing galls examined, but they have been recorded in other galls (Mani, 1964). Mani stated that as the gall approaches the maturation stage, cell proliferation slows down and finally ceases. When the *D. polita* gall is mature and the cells have reached their maximum size, the gall formers are forced to cease feeding. The developmental morphology of the *D. polita* galls initiated later in the season is identical with that of the galls initiated in the early spring.

e) Development of *P. pirata* Modified Galls

As shown in Section IIIAd, the presence of *P. pirata* causes the *D. polita* gall to increase in size. Approximately 200 observations of *P. pirata* ovipositing were made in 1969 (see Frontispiece). If a gall cluster consisted of galls in various stages of growth, the smallest and least mature were chosen first for some difficulty is probably experienced by females attempting to oviposit in galls with the collenchyma zone developed. Most of the galls containing *P. pirata* eggs were composed of cells in the homogeneous condition. Oviposition left small scars and openings on the outside of the gall. Sections of galls collected after *P. pirata* attack show channels cut into the gall's interior (Fig. 36). Tissues lining the areas damaged by the ovipositor always stained darker than the surrounding tissue suggesting that a fluid may have been injected







Figs. 36-38. Diplolepis polita galls modified by Periclistus pirata. 36. Immature gall damaged by ovipositor of Periclistus pirata. Collected June 5, 1969. 37. Gall tissue influenced by feeding of Periclistus pirata larva. Cells nearest the larva are closely packed, smaller, and darker in colour than other gall cells. Collected June 20, 1968. 38. Periclistus pirata larva surrounded by nutritive zone cells. Collected July 4, 1969. (a) tissue damaged by ovipositor; (b) Periclistus pirata eggs; (c) Periclistus pirata larva; (d) inner chamber; (e) line of tissue fusion.

at the time of oviposition. As the gall continues to grow, these channels are probably obliterated. *P. pirata* eggs were always deposited on the inside surface of the gall. Once hatched, the larvae distributed themselves evenly and commenced feeding on cells of the nutritive zone. *P. pirata* larvae restricted their feeding to one area of the gall and sucked cell contents in the manner of *D. polita* larvae. The surrounding tissue is soon affected by their presence suggesting that they secrete a cell proliferating stimulant, as do the *D. polita* larvae (Fig. 37). Cells near the larvae of *P. pirata* undergo hyperplasy but do not enlarge as do the cells influenced by *D. polita* larvae. Cosens (1912) stated that inquilines can stimulate tissues to abnormal activities, but the nutritive zone they produce is different from that produced by gall formers. Cytoplasm of cells affected by *P. pirata* becomes denser and the nuclei increase in size (Fig. 37). As the larvae continue feeding, cells slowly grow upwards surrounding them in individual chambers, similar to the manner by which the gall former is initially encased in plant tissues (Fig. 38). As the two sides of the inner chamber meet, there is tissue fusion (Fig. 38) similar to that in *D. polita* gall formation.

C) Gall Senescence and Abscission

Maturation of gall tissue affects nearly all insects associated with a gall community. Most phytophagous larvae are only capable of feeding as long as plant cells remain soft and succulent. All feeding activities of *D. polita* and *P. pirata* larvae are terminated once gall tissues mature. Gall maturation also offers gall inhabitants some protection from predators and parasites. Oviposition activities of

predators and parasites are influenced by the degree of tissue maturation. Askew (1961) found that as a gall matured, there was an increase in the time taken for a parasite to pierce the gall wall. He also measured the hardness of a gall and found that the walls of mature galls of *Cynipis divisa* Htg. were 200 times more resistant to crushing than were the walls of immature galls.

Ignoffo and Granovsky (1961) defined gall senescence as the process of turning brown due to tissue necrosis. They considered a gall necrotic when seven-eighths of the surface was brown. Mani (1964) stated that the nutritional deficiency of a leaf beyond the gall is first observed when galls begin to mature. Premature maturation of a galled organ is one of the affects of gall formation on the host. Premature maturation of galled *R. acicularis* leaflets was observed in the present study (Fig. 2). The percentage of galled leaves with necrotic tissue, found in the 11 major collections of 1969, is shown in Fig. 39. Only the spring initiated galls are represented in this graph. All galled leaves had necrotic tissue by July 28, 1969, whereas the first discolouration of normal leaves was seen in the last week of August.

D. polita galls were considered mature when at least 75% of the gall tissue was dark brown in colour. The rate of gall maturation was determined by examining the 134 galls found in the random plots described previously (Fig. 40). The first mature gall was observed June 28, 1969 and all were mature by September 6, 1969. Gall cells shrink once maturation begins resulting in a decrease of the gall's diameter. Mean shrinkage of the 134 plot galls was .82 mm. (Range from 0.1 to 2.7 mm., S.D. = 0.57). Gall shrinkage can also be observed in the 5 growth curves of Fig. 26.

Once a mature gall has fallen to the ground, it can be considered immune to attack by predators and parasites. Small rodents undoubtedly consume some fallen galls. The rate of gall abscission was also determined by examining the 134 plot galls. The first plot gall had fallen by July 14, 1969 and all had fallen by September 28, 1969 (Fig. 41). Galls growing in large clusters probably fall before galls growing singly because of their combined weight. Large gall clusters often cause the entire leaf to hang vertically (Fig. 1). Galls with their weight increased due to the presence of *P. pirata* larvae probably fall before galls containing a single *D. polita* larva. Ignoffo and Granovsky (1961) found that the gall of *Mordwilkoja vagabunda* Walsh (Aphididae) prevented the formation of an abscission layer and the gall may remain on the host for 3 years. Yasumatsu and Taketani (1967) found the first galls of *D. japonica* began falling 39 days after initiation. If the average initiation date for the *D. polita* galls can be considered May 10, then the first galls fell approximately 66 days after initiation. *D. polita* galls overwinter on the ground and because they fall before normal leaf abscission occurs, their subsequent covering by the autumn complement of leaves probably protects the gall inhabitants against the detriments of winter.

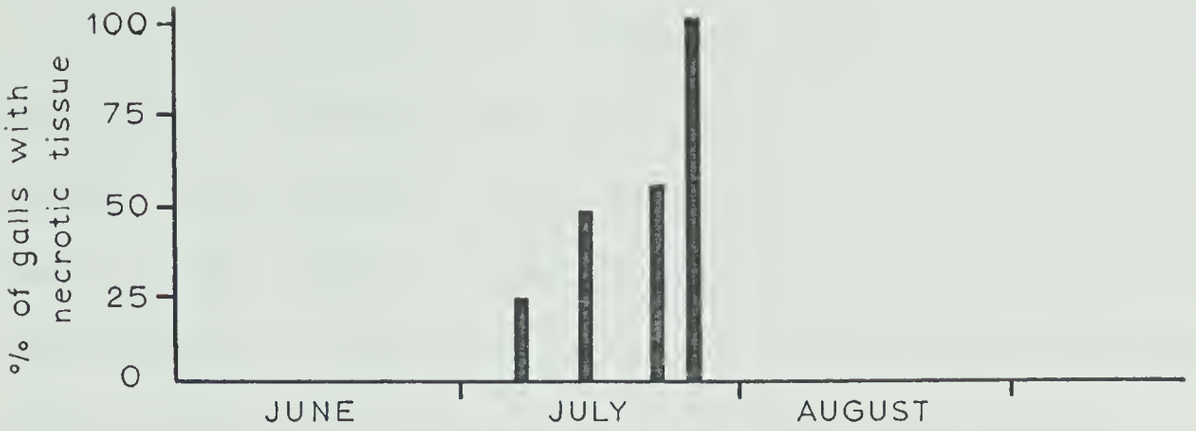


Fig. 39. Percentage of galled leaves with necrotic tissue in collections of spring initiated Diplolepis polita galls. George Lake, Alberta. 1969.

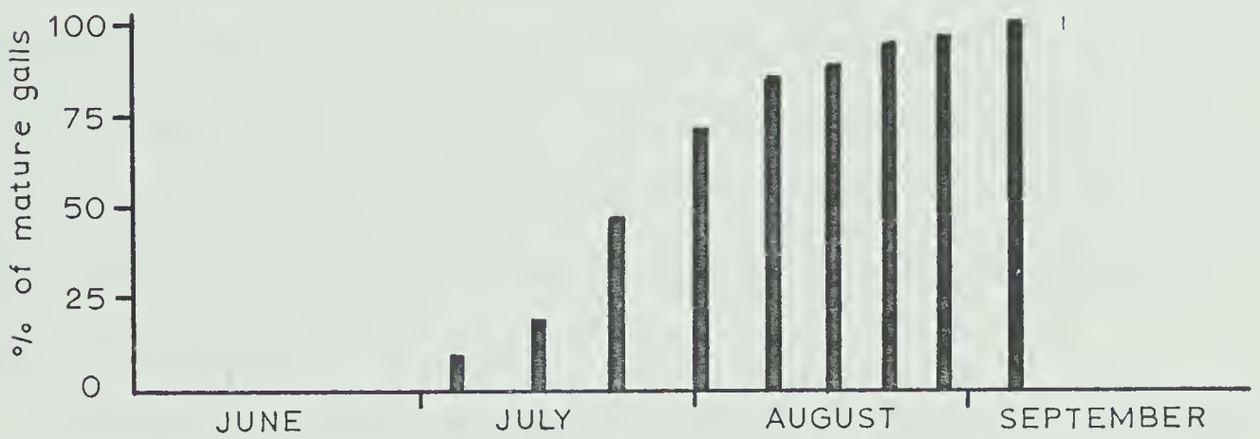


Fig. 40. Rate of gall maturation of spring initiated Diplolepis polita galls found in the 80 random plots described in Section IIIAb. George Lake, Alberta. 1969.

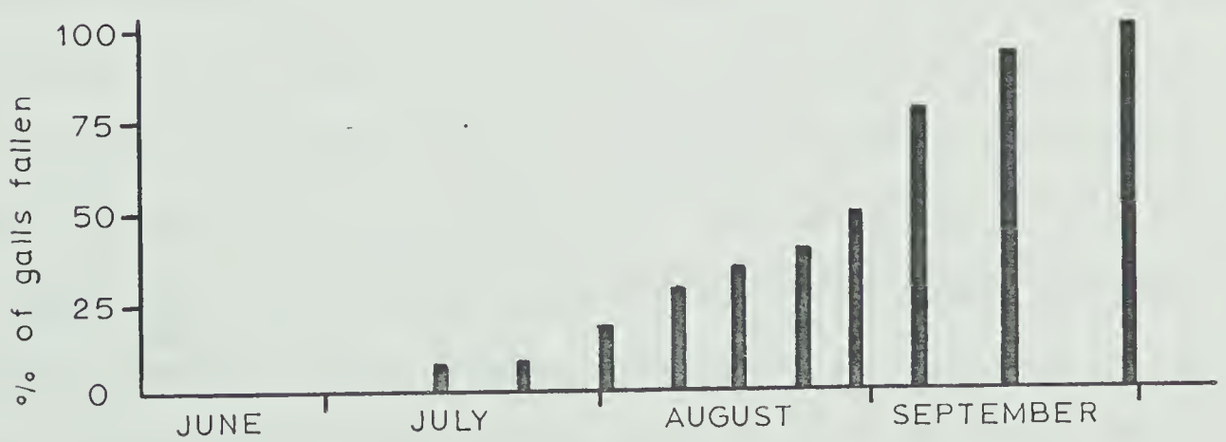


Fig. 41. Rate of gall abscission of spring initiated Diplolepis polita galls found in the 80 random plots described in Section IIIAb. George Lake, Alberta. 1969.

IV. General Discussion and Conclusions

This investigation of the *Diplolepis polita* gall and its associated inhabitants has revealed many of the basic features of cynipid gall ecology. Relationships between the various inhabitants and their hosts are intricate. The gall former is uniquely bound to the host plant, the inquiline is bound to the gall, and the remaining inhabitants are dependent upon activities of both gall former and inquiline. It is apparent that by studying cynipid galls, one has the opportunity of gaining new information about some basic concepts of biology, such as insect-plant specificity, community inter-relationships, plant developmental morphology, and genesis of important insect groups. By studying all *Diplolepis* species and their galls, employing the techniques used in this study of the *D. polita* gall, one could obtain information about the evolution of the entire complex and some of the idiosyncrasies nature has amalgamated with it.

The *Diplolepis* species complex has received little attention and the entire genus is in need of taxonomic revision. Many of the names in use are incorrect. Species have mainly been recognized by their external morphology and colour, and because the species exhibit limited variation, use of these characters only has lead to taxonomic problems. A few workers have mentioned gall structures in their descriptions of gall formers, but they made only brief mention of the external features. I suggest that gall structures could be used as valuable characters in defining species of gall formers. Structures of cynipid galls depend upon the species of insect causing them, that is, each gall former causes a specifically distinct gall. Galls induced by different species on the

same host are quite dissimilar. Other characters may be exposed by studying the communities associated with each gall. Some species of inquilines and other entomophagous inhabitants may be restricted to a single gall. Do primitive species of gall formers have smaller, simpler galls and thus simpler communities? Is the complexity of a community an indication of an advanced gall former? Does the position of the gall on either root, stem, leaf, or fruit, influence the relative complexity of the gall and thus complexity of the community?

Insect galls afford numerous opportunities for studying insect-plant host specificity and specificity of the inhabitants. It is now known how certain insects are attracted and restricted to either one or several closely related hosts, but little, if any, attention has been given to why a species is restricted to one organ of the host. Why, for example, is *D. polita* restricted to leaves? Would gall tissue develop if immature larvae were transplanted into meristematic tissues of stems or roots? *D. polita* was found only on *R. acicularis*, although *R. woodsii* often grows immediately alongside. Is *D. polita* restricted to *R. acicularis* or does only this host have tissues susceptible to galling when *D. polita* emerges? Transplanting larvae of *Diplolepis* species into meristematic tissues of other hosts may present interesting results.

Little is known about the induction of cynipid galls. Plant biochemists and morphologists would undoubtedly be interested in the chemical stimuli these insects have evolved to cause cell hypertrophy and hyperplasy. If gall formation can be induced in the laboratory, ecologists could add much information. For example, they may be able to determine whether the ability to initiate gall formation is restricted to certain larval instars. Will a monothalamous gall develop if a single larva,

normally found in polythalamous galls, is placed into susceptible tissue? Conversely, will a polythalamous gall develop if several larvae, normally found in monothalamous galls, are placed into susceptible tissue?

Data obtained on *Periclistus pirata* indicates the role inquilines can play in cynipid gall ecology. *P. pirata* takes an important position in the community and grossly modifies structures of the *D. polita* gall. Do other galls caused by *Diplolepis* species have inquilines that take similar positions in their ecology? If the structures of other galls of *Diplolepis* are as modified as those of *D. polita*, then many of the gall descriptions and illustrations now in the literature may be incorrect. Many of the descriptions may be of inquiline modified galls rather than galls caused by the gall former.

A great deal of information can be obtained on the genesis of many hymenopterans by studying cynipid galls. Can the inquilines that induce cell hyperplasy be considered as having lost the ability to cause galls, but are still restricted to galls of other species, or are they in the process of developing the ability to cause galls? Results of transplant experiments such as removing first instar larvae from galls and placing them in meristematic tissues may provide inspiring clues. If larvae of *P. pirata* were placed in galls of other *Diplolepis* species, would they be able to cause inner chamber development and other structural modifications? Two chalcidoid species, *Eurytoma longavena* and *Glyphomerus stigma* were found to be both entomophagous and phytophagous in their larval stages. It would be interesting to know if these species could complete their development on only one food. Has the phytophagous habit of these species, normally considered entomophagous, developed because of the reduced biomass in monothalamous galls, or do they exhibit the same habit in other

Diplolepis galls?

Plant morphologists stand to benefit by studying developmental morphology of cynipid galls. How these insects gain control of morphogenetic potentialities of host organs remains unknown. Galls cannot be regarded as organs, but they are more than tissue abnormalities for they have constant size and structure. An interesting problem for the morphologist would be to determine whether galls and tissues composing them can be regarded as 'new' structures, morphologically different from familiar structures. Galls of *Diplolepis* have cells and tissues unlike those normally found in the host plant. We require more information on the mechanisms that induce gall cells to divide without reference to the morphogenetic character of the host organ. It may be easier for morphologists to study processes of form determination in galls than in normal developmental processes in plants. In galls the inducing agent is not part of the physiological mechanism of the plant, but rather is introduced into the plant. If we understood how insect galls are formed, we could undoubtedly gain important clues as to normal morphogenetic processes.

In the past, most workers have taken the descriptive approach to the study of plant galls. It has been my aim to consider galls in terms of ecology rather than morphology and taxonomy. Before botanists can efficiently study developmental processes associated with insect galls, information on the ecology of associated inhabitants is required. Botanical information on the gall should be used in taxonomic studies of gall formers and associated species. By combining knowledge from various disciplines of biology, we will be in a better position to understand the evolution of cynipid galls and the intricacies of these unique

insect-plant relationships. Some of these studies I hope to do myself. Perhaps this presentation will also provide a foundation for others wishing to investigate the biology and evolution of cynipid galls.

Literature cited

Adler, H. and Straton, C.R. 1894. Alternating generations. A biological study of oak galls and gall flies. Clarendon Press, London. 198 p.

Ashmead, W.H. 1890. On the Hymenoptera of Colorado: descriptions of new species, notes, and a list of the species found in the state. Bull. No. 1 Colorado Biological Association: 1-47.

Askew, R.R. 1961. On the biology of the inhabitants of oak galls of Cynipidae (Hymenoptera) in Britain. Trans. Soc. Brit. Ent. 14(11): 237-268.

Bassett, H.F. 1890. New species of North American Cynipidae. Trans. Am. Ent. Soc. 17: 59-63.

Berland, L. 1951. Super-Famille Des Cynipoidea. Traite de Zoologie. Tome X. Premier Fascicule. Masson et C^{ie}. Paris: 882-902.

Beutenmuller, W. 1907. The North American species of *Rhodites* and their galls. Bull. Amer. Mus. nat. Hist. 23. Art. 27: 629-651.

Beutenmuller, W. 1922. Note on *Rhodites*. Bull. Brooklyn Ent. Soc. 17: 45.

Beyerinck, M.W. 1883. Beobachtungen über die ersten Entwicklungsphasen einiger Cynipidengallen. Verh. Ak. Amst. 22: 1-198.

Blair, K.G. 1944. A note on the economy of the rose bedeguar gall, *Rhodites rosae* L. Proc. S. Lond. Ent. Nat. Hist. Soc.: 55-59.

Blair, K.G. 1945a. Notes on the economy of the rose-galls formed by *Rhodites* (Hymenoptera, Cynipidae). Proc. R. Ent. Soc. Lond. (A) 20: 26-31.

Blair, K.G. 1945b. On the economy of the oak marble gall (*Cynips kollari*, Hartig). Proc. S. Lond. Ent. Nat. Hist. Soc.: 79-83.

Bugbee, R.E. 1951. New and described parasites of the genus *Eurytoma* Illiger from rose galls caused by species of the cynipid genus *Diplolepis* Geoffroy. Ann. Ent. Soc. Amer. 44(2): 213-261.

Bugbee, R.E. 1967. Revision of chalcid wasps of genus *Eurytoma* in North America North of Mexico. Proc. U.S. nat. Mus. 118. No. 3533: 433-552.

Buhr, H. 1965. Bestimmungstabellen der gallen (Zoo - und phytocecidien) an pflanzen mittelund Nordeuropas. Fischer (Jena). 1572 p.

Callan, E. McC. 1940. On the occurrence of males of *Rhodites rosae* L. (Hymenoptera, Cynipidae). Proc. R. Ent. Soc. Lond. (A): 21-26.

Caltagirone, L.E. 1964. Notes on the biology, parasites, and inquilines of *Pontania pacifica* (Hymenoptera:Tenthredinidae), a leaf-gall incitant on *Salix lasiolepis*. Ann. Ent. Soc. Amer. 57(1): 279-291.

Clausen, C.P. 1940. Entomophagous Insects. McGraw-Hill. New York. 688 p.

Cockerell, T.D.A. 1890. The evolution of insect galls. Entomologist. 23(322): 73-76.

Cook, M.T. 1902-1904. Galls and insects producing them. Parts 1 to 9. Ohio Nat. 2: 263-278; 3: 419-436; 4: 115-147.

Cook, M.T. 1909. The development of insect galls as illustrated by the genus *Amphibolips*. Proc. Indiana Acad. Sci. 25. 5: 363-367.

Cook, M.T. 1923. The origin and structure of plant galls. Science. 57(1462): 6-13.

Cosens, A. 1912. A contribution to the morphology and biology of insect galls. Trans. Canad. Inst. 9(3): 297-387.

Cosens,A. 1915. The founding of the science of cecidology. 46th Ann. Rept. Ent. Soc. Ontario: 88-93.

Cumming, M.E.P. 1968. The life history and morphology of *Adelges lariciatus* (Phylloxeridae). Can. Ent. 100(2): 113-126.

Doutt, R.L. 1959. The biology of parasitic Hymenoptera. Ann. Rev. Ent. 4: 161-182.

Eady, R.D. and Quinlan, J. 1963. Handbooks for the identification of British Insects. Hymenoptera, Cynipoidea. 8. Part 1 (a). 81 p.

Evans, D. 1967. The bisexual and agamic generations of *Besbicus mirabilis* (Hymenoptera, Cynipoidea), and their associated insects. Can. Ent. 99(2): 187-196.

Felt, E.P. 1940. Plant galls and gall makers. Comstock Publishing Company. 364 p.

Fourcroy, A.F. 1785. Entomologia Parisiensis; sive catalogus insectorum quae in agro Parisiensi reperiuntur 12(2): 233-544.

Fullaway, D.T. 1911. Monograph of the gall-making Cynipidae of California. Ann.Ent. Soc. Am. 4(4): 331-380.

Fulmek, L. 1968. Parasitinsekten der insektengallen Europas. Beitr. Ent. 18: 719-952.

Geoffroy, E.T. 1762. Histoire abrégée des insectes qui se trouvent aux environs de Paris. Paris. Durand. 2: 308.

Harper, A.M. 1959a. Gall aphids on poplar in Alberta. I. Descriptions of galls and distributions of aphids. Can. Ent. 91(8): 489-496.

Harper, A.M. 1959b. Gall aphids on poplar in Alberta. II. Periods of emergence from galls, reproductive capacities, and predators of aphids in galls. Can. Ent. 91(11): 680-685.

Harper, A.M. 1966. Three additional poplar gall aphids from Southern Alberta. Can. Ent. 98(11): 1212-1214.

Harrison, J.W.H. 1922. The egg-laying instincts of *Rhodites rosae* and certain deductions therefrom. Vasculum. Vol. 8(2): 33-37.

Hoffmeyer, E.B. 1930. Notes on some North American Callimomidae. Ent. Meded. Ned.-Indie. 17: 213-218.

Hough, J.S. 1953. Studies on the common spangle galls of oak. New Phytol. 52: 149-177; 218-228; 229-237.

Huber, L.L. 1927. A taxonomic and ecological review of the North American chalcid-flies of the genus *Callimome*. Proc. U.S. nat. Mus. 70(2663): 1-114.

Ignoffo, C.M. and Granovsky, A. 1961. Life history and gall development of *Mordwilkoja vagabunda* on *Populus deltoides*. Ann. ent. Soc. Amer. 54(5): 635-641.

Kinsey, A.C. 1920a. Life histories of American Cynipidae. Bull.Am. Mus. nat. Hist. 42: 319-357.

Kinsey, A.C. 1920b. Phylogeny of cynipid genera and biological characteristics. Bull. Am. Mus. nat. Hist. 42: 357-402.

Kinsey, A.C. and Ayres, K.D. 1922. Varieties of a rose gall wasp. Indiana Univ. Stud. 9(53): 142-171.

Kostoff, D. and Kendall, J. 1929. Studies on the structure and development of certain cynipid galls. Biol. Bull. 56: 402-459.

Krombein, K.U. 1958. Hymenoptera of America north of Mexico: Synoptic catalogue. U.S. Dept. Agric. Monogr. 2, Suppl. 1. 305 p.

Krombein, K.U. and Burks, B.D. 1967. Hymenoptera of America north of Mexico: Synoptic catalogue. U.S. Dept. Agric. Monogr. 2, Suppl. 2. 584 p.

Küster, E. 1911. Die gallen der pflanzen. Ein. lehrbuch der botaniker und entomologen. Leipzig. 439 p.

Küster, E. 1930. Anatomie der gallen. In Schröder's handbuch der entomologie. 1: 1-197.

Kuznetzov-Ugamskij, N.N. 1930. Contribution to the biology of the rose gall wasp *(Rhodites)* in Middle Asia. Rev. Zool. Russe. 10(3): 43-58.

LaRoi, G. 1968. Taiga. In Alberta, a natural history. W.G. Hardy, Editor. M.G. Hurtig. 343 p.

Lewis, W.H. 1957. An introduction to the genus *Rosa* with special reference to *R. acicularis*. Virginia Jour. Sci. 8(3): 197-202.

Lewis, W.H. 1959. A monograph of the genus *Rosa* in North America. I. *R. acicularis*. Brittonia. 11: 1-24.

Lyon, R.J. 1969. The alternate generation of *Callirhytis quercussuttoni* (Bassett). Proc. ent. Soc. Wash. 71(1): 61-65.

Malpighi, M. 1687. Opera omnia, partis secundae: de gallis. Londini 4(2): 1-44.

Malyshev. S.I. 1968. Genesis of the Hymenoptera. Methuen and Company Limited. 319 p.

Mani, M.S. 1964. Ecology of plant galls. Junk (The Hague). 434 p.

McCracken, I. and Egbert, D. 1922. California gall making Cynipidae. Stanford Stud. Biol. Sci. 3(1): 1-75.

Moser, J.C. 1965. The interrelationships of three gall makers and their natural enemies, on hackberry. Bull. N.Y. St. Mus. Sci. Serv. Bulletin No. 402. 95 p.

Muesebeck, C.F.W., Krombein, K.U., and Townes, H.K. 1951. Hymenoptera of America north of Mexico. U.S. Dept. Agric. Monogr. 2: 1420 p.

Niblett, M. 1943. The species of *Rhodites* causing pea-galls on *Rosa:* I. Entomologist. 76(956): 11-15; 34-39.

Niblett, M. 1947. The species of *Rhodites* causing pea-galls on *Rosa:* II. Entomologist. 80(1009): 121-127.

Osten Sacken, Baron R. 1863. Contributions to the natural history of the cynipidae of the United States and of their galls. Proc. Ent.

Soc. Philad. 2: 33-49.

Osten Sacken, Baron R. 1865. Contributions to the natural history of the cynipidae of the United States and of their galls. Proc. Ent. Soc. Philad. 4: 331-380.

Peck, O. 1963. A catalogue of the nearctic Chalcidoidea (Insecta: Hymenoptera). Can. Ent. Supplement 30: 1-1092.

Phillips, W.J. 1927. *Eurytoma parva* (Girault) Phillips and its biology as a parasite of the wheat joint worm, *Harmolita tritici* (Fitch). Jour. Agric. Res. 34: 743-758.

Plumb, G.H. 1953. The formation and development of the Norway spruce gall caused by *Adelges abietis* L. Bull. Conn. Agric. Exp. Sta. No. 566: 1-77.

Rohwer, S.A. and Fagan, M.M. 1917. The type-species of the genera of the cynipidae, or gall wasps and parasitic cynipoids. Proc. U.S. nat. Mus. 53: 357-380.

Smith, H.S. 1916. An attempt to redefine the host relationships exhibited by entomophagous insects. J. Econ. Ent. 9: 477-486.

Sternlicht, M. 1968. Contributions to the etiology of some galls found in Israel. Marcellia. 35(1-2): 45-63.

Stewart, A. 1914. Notes on the anatomy of the *Punctatus* gall. Amer. J. Bot. 1(10): 531-546.

Triggerson, C.J. 1914. A study of *Dryophanta erinacei* (Mayr) and its gall. Ann. Ent. Soc. Amer. 7: 1-46.

Urbahns, T.D. 1916. Life history of *Habrocytus medicaginis*, a recently described parasite of the chalcis fly in alfalfa seed. J. Agric. Res. 7(4): 147-155.

Varley, G.C. 1937. Descriptions of the eggs and larvae of four species of chalcidoid Hymenoptera parasitic on the knapweed gall-fly. Proc. R. Ent. Soc. Lond. (B) 6: 122-130.

Varley, G.C. 1941. On the search for hosts and the egg distribution of some chalcid parasites of the knapweed gall-fly. Parasitology. 33: 47-66.

Varley, G.C. 1947. The natural control of population balance in the knapweed gall-fly *(Urophora jaceana)*. J. Anim. Ecol. 16: 139-187.

Viereck, H.L. 1916. Hymenoptera of Connecticut. State Geol. Nat. Hist. Survey Bull. 22. 823 p.

Weidel, F. 1911. Beiträge zur entwicklungsgeschichte und vergleichenden anatomie der cynipidengallen der eiche. Flora. 102: 279-334.

Weld, L.H. 1926. Field notes on gall-inhabiting cynipid wasps with descriptions of new species. Proc. U.S. nat. Mus. 68(2611): 1-131.

Weld, L.H. 1952. New American cynipid wasps from galls. Proc. U.S. nat. Mus. 102(3304): 315-342.

Weld, L.H. 1957. Cynipid galls of the Pacific slope. Privately printed. 80 p.

Weld, L.H. 1959. Cynipid galls of Eastern U.S. Privately printed. 124 p.

Wells, B.W. 1916. The comparative morphology of the zoocecidia of *Celtis occidentalis*. Ohio J. Sci. 16(7): 249-298.

Wells, B.W. 1920. Early studies in the development of certain *Pachypsylla* galls on *Celtis*. Amer. J. Bot. 7: 275-285.

Wells, B.W. 1921. Evolution of Zoocecidia. Bot. Gaz. 71(5): 358-377.

Yasumatsu, K. and Taketani, A. 1967. Some remarks on the commonly known species of the genus *Diplolepis* Geoffroy in Japan. Esakia. 6: 77-87.

B29961